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Evolution of Cleptoparasitism in Anthophorid Bees as Revealed by Their Mode of Parasitism and First Instars (Hymenoptera: Apoidea)

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ABSTRACT

The methods by which cleptoparasitic anthophorid bees introduce their eggs into host nests and the anatomical and behavioral adaptations of their first instars to kill host immatures are described and analyzed. The information is derived from the literature, from new field studies, and from first instars described here. The study identifies six distinct cleptoparasitic groups: the Nomadinae, Protepeolini, Melectini, Rhathymini, Isepeolini, and Ericrocidini, and each is probably monophyletic. The lack of similar information regarding *Coelioxoides* and the Osirini (two groups recently identified as being unrelated to the Nomadinae) leaves open the possibility that the Anthophoridae may contain eight cleptoparasitic groups. It is suggested that each group represents a separate evolutionary development of cleptoparasitism in the family, although some evidence points to a common parasitic ancestor for the Isepeolini and Ericrocidini. Proof of separate evolutionary origin of cleptoparasitism in each group will rest on discovering sister-group relationships with pollen-carrying anthophorids.

Comparative descriptions of the six cleptoparasitic groups are based on descriptions (or redescriptions) and illustrations of the hospicidal first instars of the following species: *Xeromelecta (Melectomorpha) californica* (Cresson), *Melecta separata callura* (Cockerell), *Melecta pacifica fulvida* Cresson, *Thyreus lieftincki* Rozen, *Zacosmia maculata* (Cresson), *Rhathymus bicolor* Lepeletier, *Isepeolus viperinus* (Holmberg), *Aglaomelissa duckei* (Friese), *Mesoplia rufipes* (Perty), *Ericrocis lata* (Cresson) or *pintada* Snelling and Zavortink. Illustrations of first instar *Triepeolus grandis* Friese, *Townsendiella pulchra* Crawford, and *Protepeolus singularis* Linsley and Michener are presented to exemplify their lineages.

Females of *Aglaomelissa duckei* and *Mesoplia rufipes* are reported to introduce their eggs into host cells through small holes they make in the closures.

INTRODUCTION

This paper investigates the evolutionary relationships of the cleptoparasitic anthophorids through an analysis of (1) the mode of parasitism of cleptoparasitic taxa and (2) the anatomy of their first instars. Mode of parasitism is the manner in which the cleptoparasitic female introduces her egg into the host cell, and how the host egg or larva is eliminated, allowing the cleptoparasitic offspring to develop on the stored provisions. The first instars of all known cleptoparasitic anthophorids kill the hosts' young, and the anatomies of these hospicidal first instars reveal striking modifications to accomplish this purpose. Hence the morphology of these first instars is an integral part of the mode of parasitism. Knowledge about mode of parasitism and first instars is derived from previously published accounts and from new data presented below under Systematics of Cleptoparasitic First-Instar Anthophoridae.

Because the apomorphies used here are associated only with cleptoparasitism, the question as to what pollen-gathering groups gave rise to the cleptoparasitic lineages is beyond the scope of this study. We as yet know too little about first instars of nonparasitic bees to recognize other kinds of first-instar synapomorphies that link cleptoparasites and food-gathering lineages.

Cleptoparasitism is the relationship in which the young of one bee species feeds and develops on the food stored for the young of another species. This is different from social

parasitism in which the parasite female lives in the nest of the host species and her offspring are cared for by the female or females of the host species. In the Anthophoridae, social parasitism is found only in the Allodapini (see Michener, 1974: 227, for an overview).

Eggs of cleptoparasitic anthophorids are introduced into host cells in one of two ways: either the cleptoparasitic female enters the open cell while the host is away foraging and hides her egg by inserting it into the cell wall (and/or cell lining), or the cleptoparasite makes a small opening in the closure (or wall) of a cell that has already been sealed, inserts an egg through the hole into the cell lumen, and then reseals the opening. Presumably both mechanisms have evolved more than once in the family.

The hospicidal first instars of the cleptoparasitic anthophorids exhibit behavioral and anatomical modifications that enable them to seek out, identify, and kill host eggs or larvae. The universal (but not necessarily homologous) feature of these hospicidal larvae is attenuate, tapering, sharp-pointed, usually elongate mandibles used to dispose the hosts' young. Head capsules are modified and strengthened in various ways in association with the increased mandibular musculature and perhaps with sclerotization that shields the parasitic first instar from host larvae or competing cleptoparasitic young. Larval mobility is important for finding hosts, and in some lineages modifications of the abdominal apex (such as the development of a pygopod) are adaptations for crawling. Other lineages lack obvious anatomical modifications for crawling but still must crawl, perhaps by body movement alone. Some larvae have lateral body extensions, presumably enabling them to float on liquid provisions while they seek and kill host young. There is a spectrum of anatomical features involved with identifying host immatures (or immatures of other cleptoparasites) in a completely dark environment, most notably elongate, sensilla-bearing head appendages (antennae, palpi, and/or labral tubercles).

No female cleptoparasitic anthophorid has been observed to remove a host immature before ovipositing, and the first instar, and not subsequent instars, shows the most pronounced anatomical modifications involved with its hospicidal activities.[2] Cleptoparasites in other bee families have evolved a wider range of modes of parasitism than just those found in the Anthophoridae. Depending upon the group, parasitism may be accomplished (1) by the cleptoparasite female opening the host cell and killing and removing the host's young before she oviposits and reseals the cell (larvae nonhospicidal) (e.g., *Sphecodes*, *Hoplostelis*), and (2) by the cleptoparasite egg being introduced into an open or closed cell and one or more instars, but not the first instar, being hospicidal (e.g., *Coelioxys*, *Stelis*).

Unless stated otherwise, specimens described are in the collection of the American Museum of Natural History.

Acknowledgments

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The completeness of this study was aided by the loan or donation of specimens from the following specialists: Frederick D. Bennett, University of Florida, Gainesville; Charles D. Michener, University of Kansas, Lawrence; Robbin W. Thorp, University of California, Davis; Philip F. Torchio, USDA Bee Biology and Systematics Laboratory, Logan, Utah.

[2] Among the parasitic anthophorids, instars after the first are much more conventional in anatomy. Hence it would appear that only the first instar is capable of killing the host and battling other first-instar cleptoparasites. Certainly the first instars are the ones typically encountered assassinating host immatures. However, active opening and closing of mandibles and agile body movements of some second-stage cleptoparasites suggest that they too may be able to kill hosts and/or defend themselves.

Several versions of this manuscript were read by my colleagues. Their comments, suggestions, and criticisms substantially aided the formulation of ideas expressed in the final version. I wish to express my appreciation to them for their efforts on behalf of this report. An early version was reviewed by Byron A. Alexander, Robert W. Brooks, Charles D. Michener, Eric Quinter, Arturo Roig-Alsina, and Philip F. Torchio. A more recent draft was read by Byron A. Alexander, George C. Eickwort, Charles D. Michener, and Arturo Roig-Alsina.

HISTORICAL BACKGROUND

The taxonomic-evolutionary relationships of cleptoparasitic bees have long been recognized as a perplexing problem. Grütte (1935) provided a historical account of early studies and then attempted a comprehensive analysis of cleptoparasitism (including social parasitism) based on comparative adult anatomy. He was at a disadvantage for seveal reasons: (1) understanding of bee phylogeny at that time was limited, (2) he presupposed that similar cleptoparasitic forms arose from different but closely related pollen-collecting ancestors rather than from one another, and (3) adult features display a confusing array of evolutionary convergences. Michener's (1944) early treatment of the cleptoparasitic anthophorids, developed within a clearer picture of apoid phylogeny, was also based solely on adults. He followed Grütte's assumption that many of the nomadine taxa arose independently from primitive, no longer extant, pollen-collecting anthophorids, but he placed *Isepeolus*, *Protepeolus*, and also *Leiopodus* into a single tribe, the Protepeolini. In contrast to Grütte, Michener deduced that *Melecta* and *Thyreus* had not arisen from *Anthophora* but rather from a bee more primitive than those of any extant Anthophorini. He accorded separate tribal status to the Melectini, Rhathymini, and Ericrocidini, and regarded them as being closely related and quite distinct from the nomadine parasitic bees. He rejected Grütte's suggestion that some of the parasitic anthophorids arose from panurgines. Ten years later Michener (1954) decided that the genera included in the Osirini and Epeolini were closely allied to relatives of *Nomada* and all had arisen from a common parasitic ancestor. This group included most, if not all, those subgroups currently considered (that is, until the present study and the recent ones by Roig-Alsina, 1989, 1990, in press) to be members of the Nomadinae.

The same year Rozen (1954) published a brief description of the first instar of *Oreopasites* which Michener (1957) later compared with the newly found first instar of *Isepeolus*. Thus Michener was first to consider first instars in addressing evolutionary relationships of cleptoparasitic anthophorids, although comparisons of parasitic first instars of a number of families (including Anthophoridae) were made much earlier (Graenicher, 1905).

In the 1960s there began a series of investigations into larvae and life histories of cleptoparasitic bees by F. D. Bennett, G. E. Bohart, M. Favreau, C. D. Michener, J. G. Rozen, R. W. Thorp, P. F. Torchio, N. N. Youssef, and others. Bohart (1970) then attempted to sort out the evolutionary relationships. This effort was more successful than that of Grütte (1935) because it was based on a more solid understanding of bee phylogeny derived through studies on adults, and because it incorporated recently discovered life history information and recent treatments of immature stages by others. Bohart concluded that there were four origins of cleptoparasitic anthophorids: the Nomadinae, the Melectini, the Ericrocidini, and the Protepeolini (as represented by *Isepeolus* and *Protepeolus*). He considered the Melectini and Ericrocidini closely related but followed Rozen's (1969b) conclusion based on mature larvae that the two had a diphyletic origin. Both he and Rozen (1969b) believed that the Ericrocidini and Rhathymini had a common parasitic ancestor. However, in disagreement with Rozen (1966), he concluded that the Protepeolini had a separate evolutionary origin from the Nomadinae, primarily because of the characteristics of the mature larva of *Isepeolus* and its cocoon-spinning ability (the biology and larva of *Protepeolus* were still unknown).

The study of *Protepeolus* in nests of *Diadasia* (discovered on the grounds of the Museum's Southwestern Research Station in Arizona by K. R. and G. C. Eickwort) resulted

in a major rethinking about the relationships of *Isepeolus* and *Protepeolus* which until then had been placed in a single tribe. Rozen et al. (1978) retained both genera in the Nomadinae as early offshoots of the lineage but recognized them as distantly related to one another as well as to the remaining Nomadinae. *Protepeolus* was retained in Nomadinae on the basis of seven apomorphies pertaining to biologies and larvae. These will be discussed below. *Isepeolus* was also retained in the Nomadinae partly because of the number of similarities (presumably some synapomorphic) of its first instars to those of the Nomadinae and partly because comparative biological information was (and still is) unavailable.

Snelling and Brooks (1985) analyzed the cladistic relationships of adult Ericrocidini and Rhathymini. Their study concluded that either (1) the Rhathymini is a sister group of the Ericrocidini (suggesting a single origin of cleptoparasitism for the tribes) and the Centridini is the sister group of their common ancestor, or (2) the Rhathymini is the sister group of the Ericrocidini plus Centridini (*Centris, Epicharis*, and *Ptilotopus*) (requiring either a diphyletic origin of cleptoparasitism or an unlikely reversal to pollen gathering in the Centridini). Both hypotheses considered *Caenonomada*, a pollen-collecting South American "primitive" anthophorid, as the basal sister group of the rhathymine-ericrocidine-centridine complex. Of the two hypotheses, they favored (1) because of the similarity in the male terminalia of the Ericrocidini and Rhathymini and because the second hypothesis required 11 convergences between the two tribes. The first hypothesis was also in agreement with Rozen (1969b) and Bohart (1970). However, Snelling and Brooks pointed out that there are 12 adult convergences between melectines and the ericrocidine-rhathymine bees so that 11 is not an unlikely number of convergences between unrelated cleptoparasitic bees.

When I initiated the present project, three evolutionary origins of cleptoparasitism were recognized among the Anthophoridae: (1) Nomadinae (including *Isepeolus, Protepeolus, Coelioxoides, Epeoloides, Parepeolus*, and *Osiris*); (2) Melectini; and (3) Ericrocidini–Rhathymini.

However, during the course of the present investigation, Arturo Roig-Alsina independently pursued a revealing series of studies on adults of a number of groups of Nomadinae. He (Roig-Alsina, 1989) concluded that *Epeoloides, Parepeolus*, and *Osiris* were related, should all be placed in the Osirini in the Anthophorinae, and thus indicated that their cleptoparasitism had a separate origin from that of the Nomadinae. Roig-Alsina (1990) placed *Coelioxoides* in the Tetrapediini (Anthophorinae), an indication that it too was a separate evolutionary excursion into cleptoparasitism. We do not yet know the mode of parasitism of either *Coelioxoides* or the Osirini, and their immatures have not been collected. When this information is forthcoming it will be a test of the validity of the present analysis.

In yet another study, Roig-Alsina (in press) concluded that the monophyly of Nomadinae in the broad sense, that is, including the Protepeolini and Isepeolini, was not supported by his analysis of adult features, but, exclusive of these two tribes, it was monophyletic. This conclusion coincides with the analysis presented in this paper.

Recently Alexander (1990) compared a cladistic analysis of 15 genera of the Nomadinae including *Isepeolus* and *Protepeolus* based on mature larvae (from the work of Rozen et al., 1978) with a similar analysis based on adults. One result he found was that *Isepeolus* and *Protepeolus* form a monophyletic group based on adults, but this was not supported by analysis of mature larvae. When he combined larval and adult characters in a single analysis, the results closely resembled those based on larval characters alone, i.e., *Isepeolus* and *Protepeolus* formed separate basal clades of Nomadinae. This result is consistent with the conclusion presented below. The crux of the problem in studies by Rozen et al. (1978) on mature larvae and by Alexander (1990) on adults and mature larvae was the initial assumption that the Nomadinae in the broad sense is monophyletic. The present study reevaluates the presumed biological and last-instar anatomical synapomorphies used by Rozen et al. and Alexander to define the Nomadinae in the broad sense (see treatments of Isepeolini and Protepeolini in next section).

TABLE 1

Comparison of the Mode of Parasitism and of Anatomical Features of First Instars of Cleptoparasitic Anthophorids About Which Information Is Available

(See text for explanation of coding of character states.)

Character	1. Nomadinae	2. Protepeolini	3. Melectini	4. Rhathymini	5. Isepeolini	6. Ericrocidini
0. Introduction of Cleptoparasite Egg into Host Cell	1 Into open cell while host female foraging	1 Into open cell when host female foraging	2 Through closure after cell is closed	2 Through closure after cell is closed	? Unknown	2 Through closure after cell is closed
1. Egg Deposition	1 Embedded in cell wall	1 Embedded in cell wall	2 Free in cell, usually adhering to closure	2 Free in cell, adhering to closure	? Unknown	2 Free in cell, adhering to closure
2. Head Shape	1 Prognathous, rarely (*Townsendiella*, *Neolarra*) somewhat hypognathous	0 More or less hypognathous	1 More or less prognathous	0 Hypognathous	1 Prognathous	1 Prognathous
3. Parietals	0 Not swollen to somewhat swollen just in front of posterior head margin	1 Extending upwards and backwards	0 Normal, unmodified	2 Swollen, globose	0 Not swollen	0 Not swollen
4. Ventral Sclerotized Postoccipital Bridge	1 Present, not fused with labiomaxillary region	0 Absent	2 Present, fused with labiomaxillary region	1 Present, not fused with labiomaxillary region	2 Present, fused with sclerotized labiomaxillary region	2 Present, fused with sclerotized labiomaxillary region
5. Head Sclerotization	0 Ending at posterior margin	0 Ending at posterior margin	0 Ending at posterior margin	0 Ending at posterior margin	1 Extending onto prothorax	0 Ending at posterior margin
6. Cranial Band of Spinulae	0 Absent	0 Absent	1 Distinct	0 Absent	0 Absent	0 Absent
7. Troughlike External Hypostomal Groove	1 Present, at least in most cases	0 Absent	1 Present	0 Absent	0 Absent	0 Absent, except in *Ericrocis*
8. Angle of Posterior Margin of Head to Hypostomal Groove	0 Right angles or rarely obtuse	1 Broadly curved	0 Variable	2 Nearly straight	? Impossible to interpret	0 Right angle
9. Antennal Size	1 Almost always small, obscure	0 Low but distinct swelling	2 Large, elongate	1 Scarcely evident	0 Small, well defined	2 Large, projecting
10. Antennal Shape	0 Not flattened	0 Not flattened	0 Not flattened	0 Not flattened	1 Dorsoventrally flattened	1 Slightly to moderately dorsoventrally flattened
11. Antennal Fusion	1 Fused with head capsule	1 Fused with head capsule	0 Set off by ring from head capsule	1 Fused with head capsule	1 Fused with head capsule	1 Fused with head capsule
12. Labrum	1 Nonsclerotized, not fused with clypeus	0 Sclerotized, articulating with clypeus	2 Sclerotized, fused with clypeus	0 Perhaps faintly sclerotized, not fused with clypeus	2 Sclerotized, fused with clypeus	2 Sclerotized, fused with clypeus
13. Labral Tubercle(s)	1 Paired, long to very long, separately articulating	2 Three pairs, fixed to labrum	1 Paired, nonarticulating	1 Paired, nonarticulating	3 Single median	? Vague at best
14. Mandible	1 Moderately long to very long	0 Not elongate	1 Moderately long	1 Moderately long	1 Very long, slender	1 Long, robust
15. Labiomaxillary Sclerotization	1 Present mesad of hypostomal grooves but absent in middle	0 Absent	1 Somewhat on sides and behind palpi	1 Only on sides of maxillae	2 Complete	2 Complete
16. Labium and Maxillae	1 Extensively fused	0 Separate	0 Separate	0 Separate	1 Extensively fused	1 Extensively fused
17. Maxillary Palpus	1 Well developed, sometimes greatly elongate	2 Short, large, padlike	0 Small but distinct	3 Evident only because of sensilla	3 Scarcely evident	3 Scarcely evident
18. Abdominal Segment X	1 Bearing forked or trilobed, eversible pygopod	1 Bilobed	0 Rounded	1 Bilobed	2 Truncate, small, greatly fused to IX	2 Truncate, trilobed, fused to IX
19. Body Setae	0 Absent	1 Present	0 Absent	0 Absent	1 Present	0 Absent
20. Spiracles of Abdominal Segment VIII	0 Normal in position and size	0 Normal in position and size	0 Normal in position and size	0 Normal in position and size	1 Larger than preceding ones and at posterior margin of segment	1 Usually larger than preceding ones and at posterior margin of segment

EVOLUTION OF CLEPTOPARASITISM IN THE ANTHOPHORIDAE

This investigation shows that there are six distinct groups of cleptoparasitic anthophorids as revealed by their mode of parasitism and the anatomy of the first instars, exclusive of *Coelioxoides* and the Osirini (for which we have no information on mode of parasitism and anatomy of first instars). As indicated in tables 1–3, these are the Nomadinae, Prote-

peolini, Melectini, Rhathymini, Isepeolini, and Ericrocidini. If Roig-Alsina's (1989, 1990) conclusions are correct regarding *Coelioxoides* and the Osirini, then the family may contain a total of eight cleptoparasitic groups. The Nomadinae, Melectini, and Ericrocidini (the taxa for which we have information about more than one genus) are each believed to be monophyletic on the basis of the numerous shared specialized features of the included genera as revealed in table 1 and the systematics section. The general question to be addressed is whether each of the six groups treated here represent a separate evolutionary excursion into cleptoparasitism or whether two or more of them have a common parasitic ancestor. More specifically, can a study of their first instars and mode of parasitism shed light on this matter?

The only certain way of determining whether cleptoparasitism arose independently is to demonstrate through cladistic analysis that each cleptoparasitic group has a pollen-carrying sister group. This study cannot attempt such an analysis because first instars of pollen-carrying taxa are almost completely unknown, pollen-carrying taxa do not have behavior patterns (such as searching for host nests, entering host cells, killing host immatures) that can be homologized with those of cleptoparasites, and most (if not all) of the apomorphic anatomical features of the described first instars (table 1) are believed to be adaptations to hospicidal ways of life and therefore have no counterpart in nonhospicidal larvae.

Nonetheless, there is some reason to believe that most (if not all) of these six groups represent separate evolutionary origins of cleptoparasitism; **namely, there is little evidence to suggest that as a single group they are monophyletic or that any subgroup of two or more of them is monophyletic** (with the possible exception of the Isepeolini and Ericrocidini). We know that cleptoparasitism evolved independently in three bee families (Halictidae, Megachilidae, Apidae) other than the Anthophoridae, so that cleptoparasitism by itself is not a strong synapomorphy. Similarly, hospicidal larvae (with elongate, sharp-pointed mandibles) have also evolved at least three times in the Megachilidae. Many of the other specialized first-instar anatomical features associated with cleptoparasitism in anthophorids also arose in megachilid hospicidal larvae (though not always first instars). For example, first (and subsequent) instars of *Dioxys* have elongate antennae (Rozen, 1967), suggestive of those of the Melectini; hospicidal third instars of *Coelioxys* are strongly prognathous with the head capsule strongly sclerotized both dorsally and ventrally, somewhat like those of the Ericrocidini, Isepeolini, and Nomadinae (Baker, 1971). Hence homoplasy is common among these features of cleptoparasitic bees, and only when there are numerous suspected synapomorphies can we place much confidence in the monophyly of two or more groups. Table 3 lists the character states of first-instar cleptoparasitic anthophorids shared by pairs of taxa. As discussed below, only in the case of Isepeolini/Ericrocidini, with 11 shared apomorphies, is there a reasonable (though not necessarily probable) indication that they had a common parasitic ancestor.

As another suggestion that these groups are separate cleptoparasitic lineages, I analyzed them cladistically using the data in table 1. The character states were identified as plesiomorphic (0) or apomorphic (1, 2, etc.) and are presented in table 2 as a matrix (also used to derive table 3). Primitive character states (0) were based on a hypothetical ancestor. This ancestor closely parallels the description of the first instar of *Exomalopsis chionura* Cockerell[3] (Rozen, 1957), although the antenna of *E. chionura* is somewhat more pronounced than that of some other known first-instar, pollen-carrying anthophorids. All multistate characters were coded nonadditive, and autapomorphies (characters 5, 6) were deleted. With James S. Farris's Hennig86 program using the implicit enumeration command, the following single most parsimonious tree topology was produced: (Protepeolini (Nomadinae (Rhathymini (Melectini (Isepeolini + Ericrocidini))))), length 40,

[3] At the time the first instar of *E. chionura* was described, we were unaware that first instars of many, if not all, nonparasitic anthophorids are encased in the egg chorion and that the second instar is the stage the crawls away from the chorion. Hence the description may refer to the second instar. However, observations on other primitive anthophorids (including *Exomalopsis sidae* Cockerell and *Ancyloscelis wheeleri* (Cockerell) show that first and second instars of nonparasitic species are quite similar.

TABLE 2
Data Matrix for Analysis of Relationships of Parasitic Anthoporidae Based on Egg Deposition Features and First Instars
(Character coding given in table 1. All multistate characters nonadditive)

	Character																				
Taxon	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
0. Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1. Nomadinae	1	1	1	0	1	0	0	1	0	1	0	1	1	1	1	1	1	1	1	0	0
2. Protepeolini	1	1	0	1	0	0	0	0	1	0	0	1	0	2	0	0	0	2	1	1	0
3. Melectini	2	2	1	0	2	0	1	1	0	2	0	0	2	1	1	1	0	0	0	0	0
4. Rhathymini	2	2	0	2	1	0	0	0	2	1	0	1	0	1	1	1	0	3	1	0	0
5. Isepeolini	?	?	1	0	2	1	0	0	?	0	1	1	2	3	1	2	1	3	2	1	1
6. Ericrocidini	2	2	1	0	2	0	0	0	0	2	1	1	2	?	1	2	1	3	2	0	1

consistency index 80, retention index 65. This tree is not intended to indicate that the included taxa are a single monophyletic clade, but rather to show the relationships of the cleptoparasitic taxa without considering their possible pollen-carrying sister taxa. Comparing the relationships of the parasitic groups based on first instars and mode of parasitism with the earlier "traditional" relationships based on adult and mature larval features reveals distinct incongruences. Before, the Protepeolini and Isepeolini were thought to be a part of the Nomadinae, and the Rhathymini and Ericrocidini were believed related. At the same time, no one had suggested that the Isepeolini and Ericrocidini might have a common ancestor. Hence, relationships suspected on the basis of certain life stages are not supported by those based on other life stages. This again suggests that evidence in support of monophyly of the cleptoparasitic anthophorid groups is weak.

As yet another line of reasoning, these six groups deposit their eggs in host cells in different ways, and each tends to possess different and distinctive suites of first-instar

TABLE 3
Derived Character States of Egg Deposition Features and First Instars of Cleptoparasitic Anthophorids Shared by Pairs of Taxa
(For explanation, see text)

Taxa	Shared derived states	No. shared states
1/2 Nomadinae/Protepeolini	0, 1, 11, 18	4
1/3 Nomadinae/Melectini	2, 7, 13, 14, 15	5
1/4 Nomadinae/Rhathymini	4, 9, 11, 13, 14, 15, 18	7
1/5 Nomadinae/Isepeolini	2, 11, 14, 15, 16	5
1/6 Nomadinae/Ericrocidini	2, 11, 14, 15, 16	5
2/3 Protepeolini/Melectini	—	0
2/4 Protepeolini/Rhathymini	11, 18	2
2/5 Protepeolini/Isepeolini	11, 19	2
2/6 Protepeolini/Ericrocidini	11	1
3/4 Melectini/Rhathymini	0, 1, 13, 14, 15	5
3/5 Melectini/Isepeolini	2, 4, 12, 14, 15	5
3/6 Melectini/Ericrocidini	0, 1, 2, 4, 9, 12, 14, 15	8
4/5 Rhathymini/Isepeolini	11, 14, 15, 17	4
4/6 Rhathymini/Ericrocidini	0, 1, 11, 14, 15, 17	6
5/6 Isepeolini/Ericrocidini	2, 4, 10, 11, 12, 14, 15, 16, 17, 18, 20	11

modifications that enable its larvae to search for, identify, and kill hosts. Each combination of characters represents a different adaptive solution that accomplishes the same end for all lineages—elimination of host or other larvae that might feed on the food supply. Once an evolutionary lineage has developed a particular set of features that makes its members successful cleptoparasites, a different set of features that accomplish the same end would not likely evolve in that lineage. Hence, different sets of characters seem to identify separate lineages that became cleptoparasitic. However, as an argument against this hypothesis, two or more of them might have arisen from a common cleptoparasitic ancestor that was highly plesiomorphic, for example, an ancestor that had no special parasitic adaptations except for a tendency to deposit its eggs in provisioned cells of other species of bees and a first instar that was slightly more aggressive than that of the host. During evolution, such a generalized ancestor might have led to lineages that became more specialized in different ways.

As stated above, convincing evidence of the relationships of these parasitic groups will be determined when and if we can identify their sister groups. However, the validity of the other lines of reasoning can continue to be evaluated. For example, if we learn that the first instar and mode of parasitism of *Coelioxoides* (whose pollen-collecting sister taxon, *Tetrapedia*, has been identified by adult synapomorphies [Roig-Alsina, 1990]) is different from those of the other parasitic anthophorid groups, credence will be given to the reasoning presented above. Similarly, if the pollen-collecting sister group of one (or more) of the parasitic groups can be identified, this too will give weight to the idea that the other groups also had evolved cleptoparasitism de novo. In both cases, association of different modes of parasitism with groups proven to have pollen-carrying sister taxa would strengthen the probability that different modes of parasitism are an indicator of separate origins of cleptoparasitism.

The following is an expansion and discussion of the information given in table 1. It assumes tentatively that four of the six groups evolved their cleptoparasitic way of life independently and gives evidence that the fifth and sixth groups (the Isepeolini and Ericrocidini) may have had a common parasitic ancestor.

(1) Nomadinae: The largest assemblage of cleptoparasitic anthophorids, this subfamily as here constituted (i.e., without *Protepeolus, Isepeolus*, and *Leiopodus*, and presumably without *Coelioxoides* and Osirini sensu Roig-Alsina, 1989) appears to form a monophyletic group, to the extent that we have knowledge of biologies and first instars of the included taxa. In all known cases (see Bohart, 1970, for early references; Ehrenfeld and Rozen, 1977; Rozen, 1971, 1977, 1984a, 1984b, 1986, 1989a, 1989b, 1989c; Rozen and Snelling, 1986; Shanks, 1978; Torchio and Burdick, 1988), the female enters the open cell of the host while the host female is foraging, inserts a small egg into the cell wall (or cell lining), often in a characteristic genus-specific way, and then departs. The hospicidal larva emerges in time to kill the host egg or early instar. The first-instar cleptoparasite possesses elongate, more or less diverging labral tubercles that are not fused to one another or to the head capsule and that presumably sense the area in front of the prognathous, often elongate head. Antennae are scarcely evident, suggesting that they do not play a significant role in host detection. Maxillary palpi, pronounced to extremely long, must acquaint the larva with the substrate beneath its head. In contrast, labial palpi are usually not evident as projections and therefore may be of little importance. Larval mobility is assisted either by an eversible, forked, posteriorly directed pygopod arising from the last abdominal segment or by a trilobed process consisting of a narrow, elongate terminal abdominal segment subtended on each side by a lobe (these lobes are perhaps homologous with the pygopod).

Mature larvae have extremely short mandibles that contrast to the often very elongate mandibles of the first instar. Their maxillary palpi are small, and labial palpi are not generally evident. This is the only group of parasitic anthophorids that does not spin cocoons (although cocoon spinning is also lacking in the single melectine genus *Thyreus* [Rozen, 1969a] and in nonoverwintering gen-

erations of *Protepeolus* [Rozen et al., 1978] and *Xeromelecta californica* [Torchio and Trostle, 1986]), and the mature larvae have a recessed labiomaxillary region, characteristic of noncocoon-spinning bee larvae.

Although the subfamily is believed to have derived from some primitive nonparasitic anthophorid, synapomorphies in mature larvae have not been identified to align the Nomadinae with any group.

(2) Protepeolini: Like *Isepeolus, Protepeolus* was considered an early clade in the Nomadinae by Rozen et al. (1978). Only in the Nomadinae and Protepeolini (Rozen et al., 1978) are the eggs known to be embedded in the cell wall by the cleptoparasite before the host female seals the cell. This feature was originally considered a strong synapomorphy, but now is considered a convergence because it is supported by so few other possible synapomorphies of first instars and mature larvae. This convergence may be explained as follows: all parasitic anthophorids introduce their eggs into host cells; two lineages (Nomadinae and Protepeolini) independently evolved ways of hiding eggs in *open* cells that are still being provisioned; three lineages independently found means of introducing eggs into *closed* cells.

Similarities of the first instars of *Protepeolus* and the Nomadinae can be explained as convergences because these features (as listed in table 1) tend to be associated with many other parasitic lineages. Even the bilobed abdominal segment X, which suggests a pygopodlike nomadine structure, appears in two other lineages.

Only two features of the mature larvae suggested a relationship between *Protepeolus* and the Nomadinae (Rozen et al., 1978): the modified position of the posterior tentorial pits and the short mandible with simple apex and reduced cusp.

Features are not known that might align the Protepeolini with one or more extant groups of pollen-collecting anthophorids, and the tribe should be assigned to the Anthophorinae for the time being.

(3) Melectini: Females of all known melectine genera oviposit through small openings made in the closures of sealed host cells (see Bohart, 1970, for early references; Torchio and Trostle, 1986). The first instars of the Melectini described here reaffirm that the tribe is monophyletic and that it is not closely akin to other parasitic Anthophoridae. The band of spinulae extending across the vertex from the mandibular bases and large conical antennae appear to be unique apomorphies for the group. The basal membranous ring of the antenna is also unique among parasitic anthophorids. This feature is probably plesiomorphic, so that its absence in other parasitic groups must be convergent.

Bohart (1970) hinted that the Melectini and Ericrocidini might be related. Although the similarities between the two (8, in table 3) are the second highest number of shared character states among the cleptoparasitic lineages, they are not strong apomorphies.

Both Michener (1944) through studies of adults and Rozen (1969b) who compared mature larvae concluded that the Melectini and the Anthophorini arose from a common ancestor. The present study sheds no further light on this matter.

(4) Rhathymini: Camargo et al. (1975) concluded that the mode of parasitism of *Rhathymus* was like that of the melectines, based on finding a cast chorion and first instar exuviae in situ in a cell that they also illustrated (their fig. 4B). This conclusion is supported by new information under Systematics of Cleptoparasitic First-Instar Anthophoridae, below.

One of the most surprising discoveries of the present study was that the first instar of *Rhathymus* is vastly different from all the other known cleptoparasitic anthophorids. The comparatively few shared first-instar features of *Rhathymus* and other cleptoparasites including the Ericrocidini do not support a close relationship between *Rhathymus* and the others. Rozen (1969b), Bohart (1970), and the favored hypothesis of Snelling and Brooks (1985) had concluded that *Rhathymus* and the Ericrocidini had a common parasitic origin. However, the greatly swollen hypognathous head (presumably for attachment of large mandibular muscles) of the first instar as well as the other characters presented in table 1 argue against this hypothesis unless, of course, the common ancestor was highly plesiomorphic. Separate origins of

cleptoparasitism in Rhathymini and Ericrocidini are consistent with the second hypothesis of Snelling and Brooks (1985: fig. 78B).

The relatively high number (7, in table 3) of specialized character states shared by the Nomadinae and Rhathymini are believed to be the result of convergence because features of adults and mature larvae do not support (but do not refute) a close relationships between these two taxa.

(5) Isepeolini: This tribe has been assigned to the Nomadinae by most workers, although Bohart (1970) believed it (as Protepeolini) distinct because of the features of the mature larva and its cocoon-spinning habits. Except for its hospicidal larva, other features concerning mode of parasitism are still unknown.

With our increasing knowledge of first instar parasitic anthophorids (especially the Nomadinae), it seems obvious that the striking similarities (only 5, in table 3) of first instars of *Isepeolus* and the Nomadinae are convergences that have appeared independently among many of the lineages. These include the strongly prognathous, elongate, heavily sclerotized head capsule, curved elongate mandibles, and linear body form. These are unconvincing similarities in the presence of the following differences (contrasting features of the Nomadinae in parentheses): labrum bearing single small median, probably apical[4] tubercle (paired tubercles arising from disc rather than apex of labrum); antennae, though small, sharply projecting (vague swellings); ventral surface of head completely sclerotized and all palpi absent or at least nonprojecting (labiomaxillary region membranous at least medially and maxillary palpi conspicuous, often greatly elongate); sclerotization of head capsule extending over part of prothorax (extending only to posterior margin of head); abdominal apex without pygopod (pygopod well developed, often large).

The mature larvae of *Isepeolus* and the Nomadinae differ in a number of ways: body tubercles present (absent; body often streamlined); labrum with single median, sensilla-bearing apical tubercle (paired tubercles arising from disc always present); mandibles moderately long (unusually short); larva cocoon-spinning and therefore possessing projecting labiomaxillary region and pronounced maxillary and labial palpi (noncocoon-spinning; labiomaxillary region recessed).

The large number of striking specializations (11, in table 3) of first instars of *Isepeolus* and Ericrocidini may reflect that the two taxa had a common cleptoparasitic progenitor. These features include: a heavily and completely sclerotized ventral head surface that is fused to the heavily pigmented head capsule; fusion of the labrum to the clypeus; sclerotization of the area (presumably the maxillae) between the mandibles and the mouth; distinct antennae; fusion of abdominal segments IX and X (more extensive in *Isepeolus*); and enlarged spiracles (and spiracular tracheae) (except apparently for *Ericrocis*) of abdominal segment VIII that are positioned at the rear margin of the segment. These enlarged and repositioned terminal body spiracles suggest that the larvae are semimetapneustic, perhaps an adaptation permitting the larvae to remain mostly submerged in the semiliquid provisions of their unrelated hosts (*Colletes* and *Centris*).

The features listed above appear to be strong synapomorphies because many (especially the nearly completely sclerotized head, the enlarged and posteriorly positioned spiracles, and the fusion of the terminal abdominal segments) are not known in other lineages. Furthermore, some of the apparent differences between the two taxa can be interpreted as sequences in a linear transformation series: small or large but always flattened and distinct antennae; vague narrowed paired labral tubercles or single median labral tubercle, but labrum always fused with clypeus; mandibles robust or slender but always long; greater or less fusion of terminal ab-

[4] Reexamination of the mature larva of *Isepeolus* shows that the sensilla-bearing median protuberance of the labium is apical, in contrast to the sensilla-bearing paired tubercles of mature Nomadinae which arise from the labral disc. This difference in position suggests that the tubercles of the two groups are nonhomologous. Since the labral tubercles of mature larvae are homologous with those of the first instar of the same taxon, the median tubercle of the first instar of *Isepeolus* cannot be a homolog of the paired labral tubercles of first-instar Nomadinae, no matter where they seem to arise.

dominal segments. Other differences appear to be autapomorphies of *Isepeolus*: head greatly dorsoventrally flattened, its sclerotization extending to anterior part of prothorax; and head and body setae evident.

A reexamination of the features of the mature larvae of these taxa (*Isepeolus*: Rozen, 1966; Ericrocidini: Rozen, 1969b, Rozen and Buchmann, 1990) shows a number of similarities that are plesiomorphic, such as adaptations for cocoon spinning (e.g., projecting labiomaxillary region and long palpi). Autapomorphies exist in both taxa, but no features that support or contradict a sister-group relationship can be identified. Biological attributes of *Isepeolus*, such as where and when its eggs are laid, are unknown, but once discovered may test the suspected relationships of the two taxa.

Roig-Alsina (personal commun.), after reading a preliminary version of this manuscript, commented on the possible relationships of the Isepeolini and Ericrocidini: "If they are sister taxa, Isepeolines should introduce their eggs into closed cells as Ericrocidines do. But there may be some indirect evidence to the contrary. Females of Isepeolini have modified sixth sterna which end in a sharp point and, depending on the group, may bear short or long spine-like setae. The possession of a modified tip of the abdomen is convergent with nonhomologous modifications in the Nomadinae and Protepeolini and might suggest a similar female behavior: embedding the egg into the cell wall. On the other hand at least two groups of Isepeolini have modified mandibles, elongate and sharp in the *Melectoides senex* group and tridentate in most *Isepeolus*. I wonder if they might be used to break into closed cells."

(6) Ericrocidini: Information presented under Systematics of Cleptoparasitic First-Instar Anthophoridae, below, indicates that the females of at least two ericrocidine genera insert their eggs through holes made in the closures of host cells. As explained under the Rhathymini, first-instar ericrocidines are very different from first-instar *Rhathymus*, and do not support the hypothesis that the two had a common parasitic ancestor.

For reasons expressed above, the Ericrocidini and Isepeolini may have evolved from a common cleptoparasite. However, their first and last instars are quite different so that the two groups could well be considered separate but related tribes in the Anthophorinae.

SYSTEMATICS OF CLEPTOPARASITIC FIRST-INSTAR ANTHOPHORIDAE

Methods

Most specimens used in this study were collected from host nests either as first-stage larvae or as eggs which then hatched in rearing containers. To avoid postmortem changes, specimens are best studied and drawn when freshly killed, but rarely was this convenient. Those collected by me were fixed in Kahle's solution and later transferred to 70% ethanol for storage. So as to be easily retrieved, very small larvae were placed into microvials (e.g., 25 × 8 mm) stoppered with cotton and enclosed in 4-dram storage vials with neoprene stoppers.

Study procedures for first instars were similar to those used for mature larvae with certain exceptions dictated by their small size, rarity (some taxa known from single specimens), and the often hydrofuge nature of their body integument, which makes it difficult to submerge cleared specimense in liquids. Before drawing and clearing, the external anatomy of each larva was examined. While submerged in alcohol, the uncleared specimen was then drawn with a camera lucida and stereoscopic microscope. Next, the head was severed, and both body parts boiled for approximately 5 minutes in a solution of potassium or sodium hydroxide until internal tissue became semitransparent. Some specimens were then kept in an hydroxide solution at room temperature several hours or overnight to reduce the internal tissue further. As required, a specimen was usually briefly boiled again to further remove tissue. During clearing, a specimen was closely monitored without being removed from solution. I did not extensively squeeze or mechanically remove body tissue because manipulation might have altered the body shape, made it difficult to submerge the hydrofuge integument below the surface film, and/or in some cases resulted in the integument folding and clinging to itself.

After clearing, large specimens were trans-

ferred directly to water, but small ones were placed in a watch glass containing a hydroxide solution. Transferring specimens by forceps from one solution of hydroxide to another (even of different temperature) allowed them to submerge easily rather than to float and flatten on the surface film as often happened if they were placed directly into pure water. The hydroxide solution was replaced with pure water by dropper, and the process was repeated several times to eliminate as much hydroxide as possible. I avoided acidulated water because it might have caused residual tissue to coagulate and distort soft exoskeletons. The head and body were then transferred to glycerin in a suitably labeled Wheaton culture slide for study by stereoscopic and compound microscope. Details of sensilla, integumental sculpturing, and internal anatomy were added to the pencil drawings. Inked final illustrations were copied on vellum laid over the pencil drawings. Specimens were subsequently retained indefinitely in glycerin on culture slides.

Except for the Nomadinae and Protepeolini, one species of each of the other parasitic lineages is fully described in the following sections. Hence descriptions of first instars of related species discovered in the future can be prepared by reference to these descriptions and without reference to the tribal/subfamilial descriptions. Tribal/subfamilial descriptions are based on the species descriptions and identify those features that seem to be important for differentiating and assessing the relationships of the higher taxa with our present knowledge. The numerous species of Nomadinae are not treated individually, but await study. As indicated below, they can be described at the tribal/subfamilial level because of previous studies of some groups and because of a survey of the collections available to me. The larva of *Protepeolus singularis* Linsley and Michener was described recently (Rozen et al., 1978), and is not redescribed here.

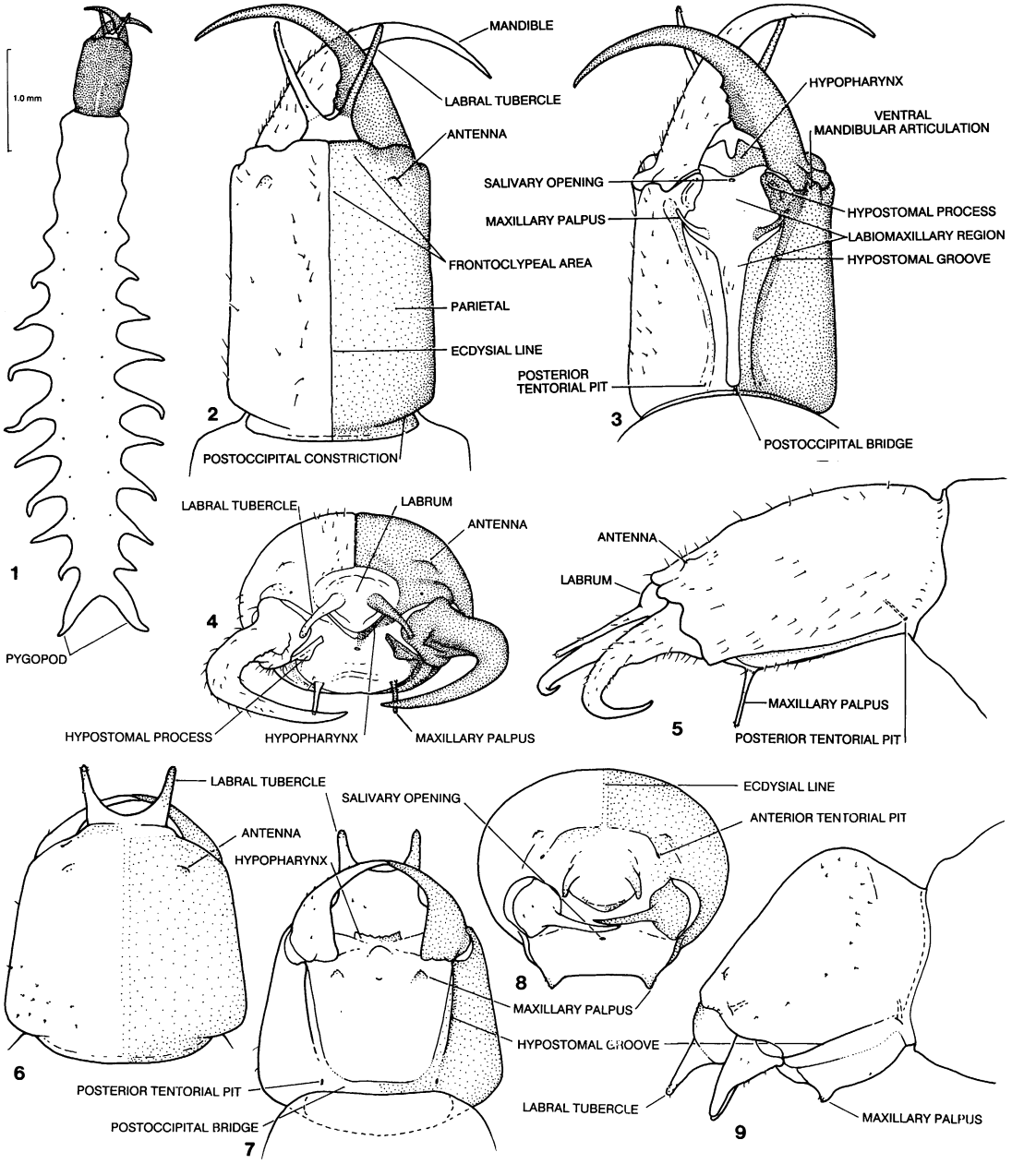
Description of the Nomadinae Based on First Instars

Figures 1–9

Although first stage larvae of most Nomadinae have yet to be studied in detail, those of *Oreopasites* (Rozen, 1954), *Kelita* (Ehrenfeld and Rozen, 1977), and a number of species of *Triepeolus* and *Epeolus* (Rozen, 1989b) were described and illustrated. The following account is based in part on the previously published descriptions and in part on a survey of representatives of the genera listed under Genera Studied, in the collections of the American Museum of Natural History. These larvae show considerable variation (compare, for example, figs. 2–5 and figs. 6–9) and, when studied fully, will probably help clarify relationships within the subfamily. The numerous shared features, mostly derived, suggest that the group is monophyletic and represents a single evolutionary transformation into cleptoparasitism.

Illustrations of two taxa are presented to demonstrate the similarities and disparities in first-instar features in the subfamily: *Triepeolus grandis* Friese (figs. 1–5; see also Rozen, 1989b) and *Townsendiella pulchra* Crawford (figs. 6–9; illustrations based on one specimen, 11 mi southwest of Congress, Yavapai Co., Arizona, April 30, 1990 [J. G. Rozen and R. J. McGinley], from nest of *Hesperapis larreae*).

Head: Shape prognathous (less so in *Neolarra, Townsendiella* (fig. 9), *Neopasites*), more (fig. 2) or less (fig. 6) elongate, not strongly dorsoventrally flattened (in contrast to *Isepeolus*); parietals not swollen (e.g., *Epeolus, Triepeolus* (fig. 5), *Oreopasites, Nomada*) or more or less swollen just in front of posterior margin of head (e.g., *Neopasites, Brachynomada, Holcopasites, Neolarra, Townsendiella*, fig. 9). Integument of head capsule heavily sclerotized, faintly to deeply pigmented; sclerotization ending posteriorly at rear of head, not extending over anterior part of thorax (as in *Isepeolus)*; capsule with sensilla either nonsetiform or more rarely represented as long, fine setae (e.g., *Neolarra, Brachynomada,* Epeolini); head sensilla not borne on small tubercles; capsule without ring of sharp-pointed spinulae across vertex (as found in Melectini). Tentorium complete in some cases but mostly unstudied; posterior tentorial pit in or below hypostomal groove; conspicuous troughlike hypostomal groove externally at least on some taxa (figs. 3, 7) (similar to that of Melectini); sclerotization of head capsule often extending mesad of each groove but



Figs. 1–5. *Triepeolus grandis*, first instar. **1**. Entire body, dorsal view. **2-5**. Head, dorsal, ventral, frontal, and lateral views.

Figs. 6–9. *Townsendiella pulchra*, head of first instar, dorsal, ventral, frontal, and lateral views. Scale refers to figure 1. Figures 1-5 modified from Rozen, 1989a.

these extensions separated by median V-shaped membranous area (labiomaxillary region) or at least labiomaxillary region never entirely sclerotized; however, head posteriorly often, if not invariably, with ventral sclerotized postoccipital bridge; pleurosto-

mal and epistomal ridges often not defined because of heavy sclerotization of head capsule; distinct pale median dorsal ecdysial line evident on those species with pigmented head capsules; posterior margin of head capsule nearly at or at right angle with hypostomal groove as seen in lateral view, rarely (e.g., *Brachynomada*) at obtuse angle. Each antenna usually a small vague protrusion fused to head capsule, rarely more distinct, but never a large projection (as in Melectini and Ericrocidini). Labrum (figs. 4, 8) unsclerotized except for a single pair of labral tubercles; these tubercles elongate, usually apically diverging, articulating independently. Mandible often very long, attenuated, slender apically and either slender or stout basally; inner edge usually smooth but sometimes (e.g., Epeolini, figs. 2, 3) bearing teeth or sharp-edged projections. Labiomaxillary region fused, membranous except for sclerotized maxillary palpus in some cases; maxillary palpus pronounced, ranging from being as long as basal diameter (fig. 9) to being many times longer than basal diameter (e.g., *Brachynomada*, Epeolini, fig. 5); labial palpus usually not projecting and therefore not detectable except perhaps for grouping of sensilla but present in some groups (e.g., *Holcopasites, Nomada*). Hypopharynx (figs. 3, 7) usually if not invariably a transverse sclerotized plate that is V-shaped, medially notched, or curved along its anterior edge.

BODY: Form elongate, straight, usually tapering posteriorly, with (fig. 1) or usually without (Rozen, 1989b: figs. 23, 27, 29, 30, 35, 37) lateral tubercles, occasionally (*Townsendiella*) with paired ventrolateral tubercles on abdomen; abdominal segment X bearing eversible bifurcate pygopod; rami of pygopod posterolaterally directed, short (e.g., *Oreopasites, Pasites, Neolarra*) or long (e.g., *Pseudodichroa,* Epeolini, fig. 1); occasionally (e.g., *Townsendiella, Nomada*, and apparently *Paranomada*) segment X narrow, projecting posteriorly so that abdomen appearing apically trilobed (lateral lobes presumably homologous with pygopod); prothorax sometimes protruding ventrally. Integument without setae, usually with patches of short, fine, inconspicuous spicules. Thoracic spiracles present (e.g., *Pseudodichroa*) or absent (Epeolini); spiracles on abdominal segments I–VIII dorsal, all approximately same size; those of segment VIII in normal position, not at posterior margin of segment as in known Ericrocidini. Position of anus unknown.

GENERA STUDIED: First instars of one or more species of the following genera were examined: *Brachynomada, Caenoprosopis, Caenoprosopina, Epeolus, Holcopasites, Kelita, Neolarra, Neopasites, Nomada, Oreopasites, Paranomada, Pasites, Pseudodichroa, Townsendiella,* and *Triepeolus*.

REMARKS: This diverse subfamily, the largest cleptoparasitic group of anthophorids, will be treated in a subsequent study to shed light on the interrelationships of the included taxa.

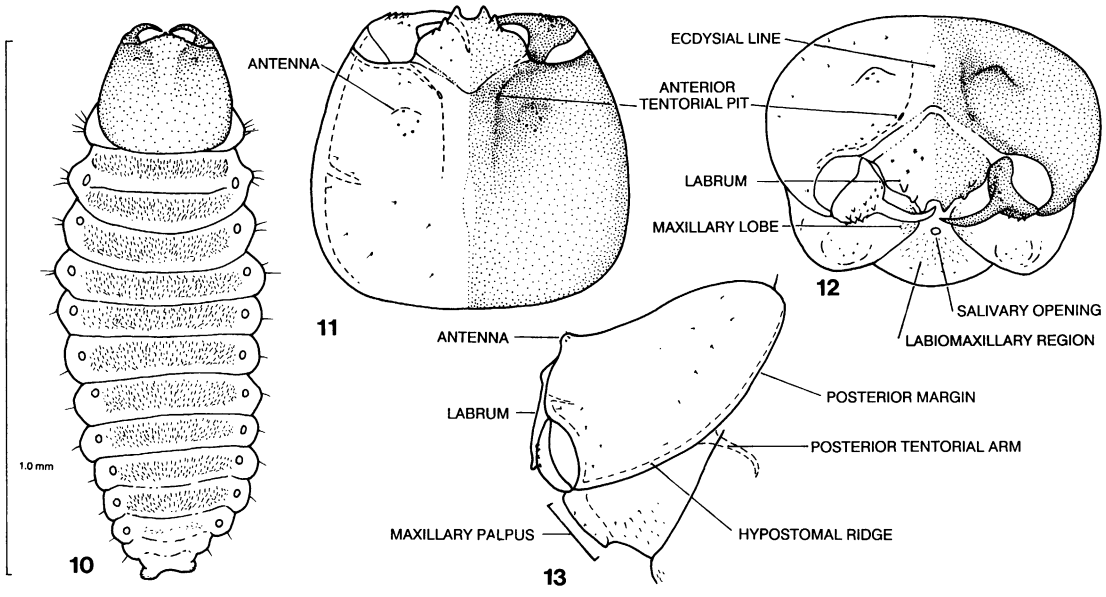
DESCRIPTION OF THE PROTEPEOLINI BASED ON THE FIRST INSTAR

Figures 10–13

This description is based on the material used by Rozen et al. (1978) in their treatment of the larvae and biology of *Protepeolus singularis* Linsley and Michener.

Head (figs. 11–13; see also Rozen et al., 1978): Shape more or less hypognathous;[5] parietals extending posterodorsally so that height of head from vertex at posterior margin of head to posterior mandibular articulation nearly twice as long as distance from posterior tentorial pit to apex of clypeus as seen in lateral view (fig. 13), hence capsule appearing shallow by comparison with all other known cleptoparasitic anthophorids; capsule not strongly flattened dorsoventrally as in *Isepeolus*. Integument of head capsule heavily sclerotized and darkly pigmented; sclerotization ending posteriorly at rear of head; many sensilla setiform, moderate in length; those on mandibular bases apparently borne on small tubercles; capsule without band of sharp-pointed spinulae across vertex. Tentorium possibly complete, but anterior arms thin; anterior pits distinct; posterior pits distinct, arising from hypostomal ridges and posterior thickening of head; hypostomal ridge well developed; external groove not

[5] Interpretation of this feature depends on the orientation of the head capsule in lateral view. If it is positioned so that the hypostomal groove is horizontal, the head becomes more prognathous. If oriented so that the posterior margin of the head is vertical, the head becomes more hypognathous.



Figs. 10–13. *Protepeolus singularis*, first instar. **10**. Entire body, dorsal view. **11-13**. Head, dorsal, frontal, and lateral views. Scale refers to figure 10. Figure 13 modified from Rozen et al., 1978.

troughlike (as in some if not all Nomadinae, *Ericrocis*, and Melectini); sclerotization of head capsule not extending below (mesad of) hypostomal ridges (labiomaxillary region completely unsclerotized); pleurostomal ridge moderately well developed at least near anterior mandibular articulation; epistomal ridge laterad of anterior tentorial pits moderately well developed but apparently absent mesad of pits; distinct pale median dorsal ecdysial line present; posterior margin of head capsule not forming sharp angle with hypostomal ridge but appearing as a gently curved extension of it, as seen in lateral view (fig. 13). Each antenna a low but distinct swelling fused with and gradually arising from front of head. Labrum (fig. 12) a distinct sclerotized plate bearing three pairs of fixed (nonarticulating) tubercles; labral plate distinct from and articulating with clypeus; clypeus presumably very short. Mandible (Rozen et al., 1978: figs. 13, 14) short (by comparison with those of Nomadinae and Ericrocidini) but seemingly long because of very slender, curved, fanglike apical part that curves into buccal cavity when mandible closed; mandibular base stout; inner edge smooth. Labiomaxillary region (fig. 12; see also Rozen et al., 1978: fig. 23) completely membranous; maxilla distinct from labium (not fused); maxilla with large orally directed apical lobe bearing numerous moderately short setiform spicules; maxillary palpus borne ventroapically as short but large, oval, padlike structure; labium covered with posteriorly directed, moderately short, setiform spicules; palpus apparently nonprojecting, flattened, rather large, nonspiculated area bearing a few sensilla on ventral surface of labium. Hypopharyngeal area apparently not defined because salivary opening very close to mouth (also not defined in last larval instar, Rozen et al., 1978).

BODY: Form (fig. 10; see also Rozen et al., 1978: figs. 8, 9) moderately robust, straight, without tubercles; abdominal segment X with two lateral posteroventrally directed lobes, possibly but not certainly homologous with nomadine pygopod (muscle attachment unknown) and/or with somewhat similar structures in Rhathymini. Integument with scattered setae (those on sides of thoracic and abdominal segments long) as well as extensive areas of long setiform spicules (Rozen et

al., 1978: fig. 24). All spiracles present, in normal position, approximately same size. Anus not detected.

GENUS STUDIED: *Protepeolus*.

DESCRIPTION OF THE MELECTINI BASED ON FIRST INSTARS

HEAD: Shape more or less prognathous, not as strongly so as in Nomadinae or Ericrocidini, not dorsoventrally flattened; parietals shaped normally for bee larva. Integument of head capsule sclerotized but at most only faintly pigmented; sclerotization ending at posterior margin of head; sensilla obscure, nonsetiform, but at times borne on distinctive small tubercles; linear band of spinulae (small tubercles bearing apical cluster of microscopic projections, figs. 15, 18, 19, 22) ringing head from mandible to mandible over vertex. Tentorium complete; anterior pits distinct; posterior tentorial pits arising from rear of hypostomal groove; internal hypostomal ridge not well developed but conspicuous troughlike hypostomal groove (fig. 16) externally, suggestive of that of Nomadinae; weak ventral sclerotization of head (fig. 16) mesad of (below) hypostomal groove and behind palpus; rest of labiomaxillary region unsclerotized; pleurostomal ridge weakly developed; epistomal ridge weakly developed laterad of anterior tentorial pits, absent mesad of pits; pale dorsal median ecdysial line scarcely evident because of lack of pigmentation of head capsule; posterior margin of head capsule at right angles to hypostomal groove (*Xeromelecta*) or at obtuse angle because of curving of ridge (*Thyreus, Zacosmia*). Each antennal papilla (figs. 17, 18, 21) separated from head capsule by basal ring, not fused to head as in other known cleptoparasitic anthophorids; antenna large, elongate forward-curving, tapering apically, sometimes with sensilla borne on tubercles. Labrum (fig. 15) sclerotized, fused with clypeus bearing nonarticulating rounded or acute paired apical tubercles. Mandible moderately short by comparison with that of Ericrocidini and many Nomadinae, but not as short as that of Protepeolini, gradually tapering apically from rather stout base, not with apical part fanglike and abruptly narrower than base as in Protepeolini; inner edge smooth, without teeth or projections. Labiomaxillary region membranous except for sides of maxillae and base of labium; region not greatly fused apically; maxilla with elongate, spiculate (except apparently in *Melecta*), adorally directed apical lobe; maxillary and labial palpi small but distinct papillae. Hypopharynx bilobed, nonspiculate, unsclerotized.

BODY: Form (figs. 14, 23, 28, 33) moderately elongate, straight, without lateral body tubercles; abdominal segment X rounded, without tubercles or other obvious structures for crawling. Integument without setae, usually with patches of fine spicules. All spiracles present and normal in location. Anus apparently small transverse slit, apical in position, except presumably dorsal in position in *Melecta pacifica fulvida*.

GENERA STUDIED: *Xeromelecta, Melecta, Thyreus,* and *Zacosmia*.

REMARKS: The distinctive hypostomal groove found throughout this tribe is strikingly similar to that of the Nomadinae. Presumably it had a separate evolutionary origin in each group, but its function deserves to be investigated to shed light on this matter.

Xeromelecta (Melectomorpha) californica (Cresson)

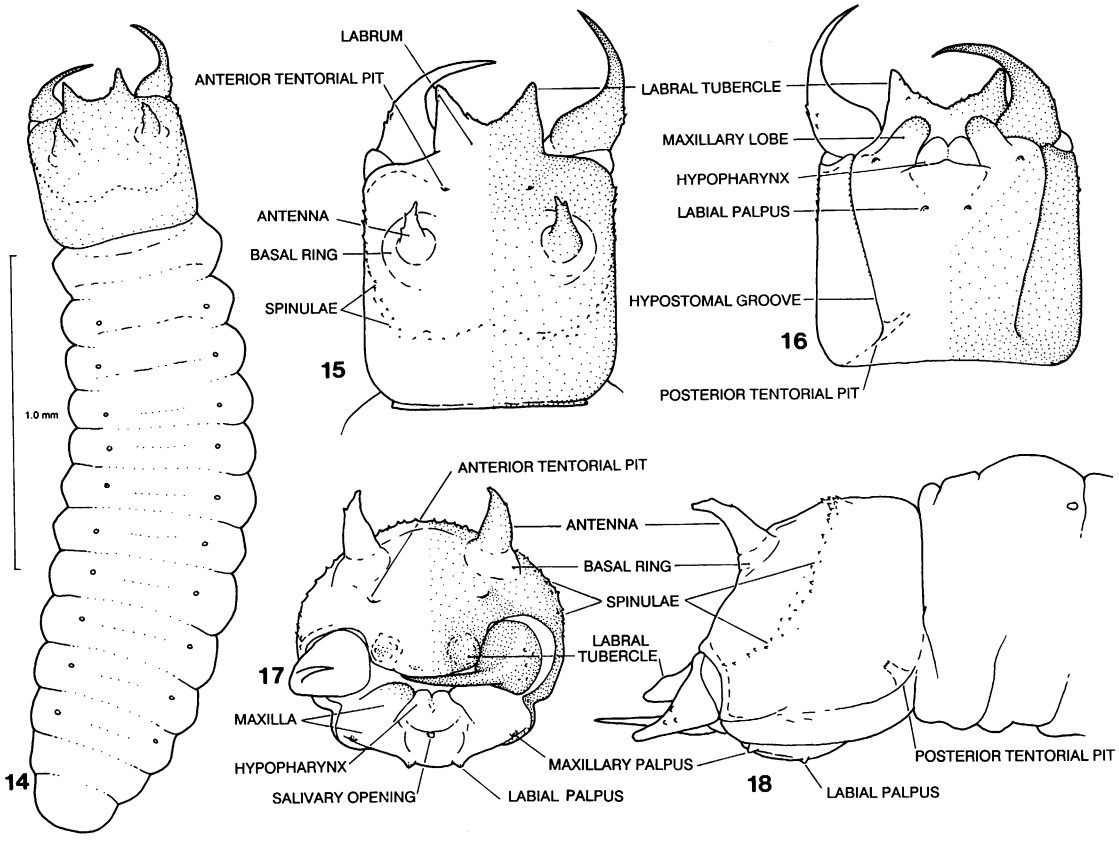
Figures 14–22

The first instar of this species has not been described before although Bohart (1970) and Torchio and Trostle (1986) presented photographs of it.

DIAGNOSIS: This species differs from the first instars of *Melecta pacifica fulvida, Zacosmia maculata*, and *Thyreus lieftincki* in that its head capsule is more elongate ventrally as seen in lateral view (fig. 18) and its labral tubercles are more elongate, more widely spaced apically, and larger (fig. 15). However, its head capsule (fig. 15) is less elongate and its labral tubercles (fig. 15) and antennae (figs. 17, 18) are shorter than those of *Melecta separata callura*.

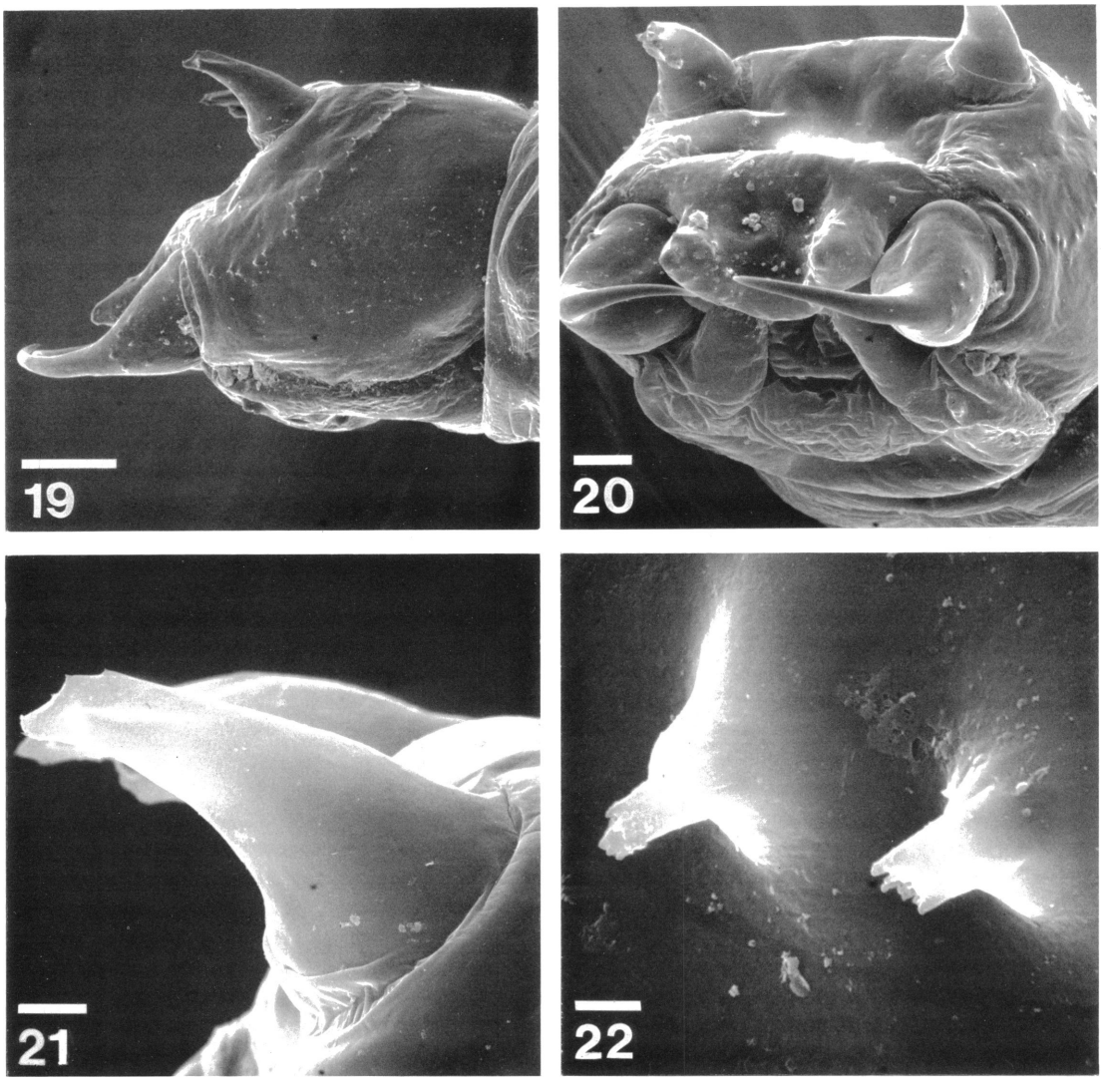
LENGTH: 2.2–2.8 mm (N = 4).

HEAD (figs. 15–18): Shape prognathous although not as strongly so as in Epeolini (Rozen, 1989b), not dorsoventrally flattened, somewhat elongate especially ventrally, and, as seen from above or below (figs. 15, 16), quadrate and nearly parallel-sided; foramen



Figs. 14–18. *Xeromelecta californica*, first instar. **14.** Entire body, dorsal view. **15–18.** Head, dorsal, ventral, frontal, and lateral views. Scale refers to figure 14.

magnum narrower than width of capsule. Integument of head capsule thickly sclerotized but only faintly pigmented; apices of mandible darkly pigmented; ventral integument between hypostomal grooves somewhat sclerotized and faintly pigmented posterior to palpi (fig. 16); other areas including hypopharynx unsclerotized. Visible setae absent; head capsule with a narrow ring of sharp-pointed spinulae extending from base of mandibles across vertex (figs. 15, 18, 19, 22) (characteristic of known Melectini); integument of antennae, labral tubercles, anterior edge of labrum, and base of mandibles with many sensilla borne on small tubercles. Tentorium including dorsal arms complete, moderately developed; anterior tentorial pits moderate in size; posterior pits in hypostomal grooves; hypostomal ridge (internal) not strongly developed but external groove pronounced, extending from posterior tentorial pit to ventral mandibular articulation; this groove formed by protruding ventral surface of head and less protruding parietal; integument of groove not pebbled as in Epeolini but irregularly sculptured; sclerotization of head capsule extending mesad of grooves, as discussed above; distance between grooves relatively large compared with that of Epeolini; pleurostomal ridge moderately weakly developed; epistomal ridge weakly developed laterad of anterior tentorial pits, absent between them; pale dorsal ecdysial line only faintly visible because of lack of pigmentation elsewhere. Parietal bands not evident. Each antenna large, projecting, curving forward, separated from head by basal ring, and, as seen in frontal view (fig. 17), rising above vertex; antennal sensilla borne on small tubercles, giving antenna knurled appearance.



Figs. 19–22. Head of *Xeromelecta californica*. **19**. Lateral view. Scale = 100 microns. **20**. Frontolateral view. Scale = 50 microns. **21**. Antenna, lateral view. Scale = 20 microns. **22**. Spinulae. Scale = 2 microns.

Labral sclerotization, including that of tubercles, continuous with that of front of head capsule, so that these areas do not articulate with one another; paired labral tubercles large, conical, apically acute, and with numerous small sensilla-bearing tubercles apically and on mesial sides. Mandible elongate by comparison with that of nonhospicidal larva (though shorter than that of Epeolini), sharp-pointed, attenuate and slender apically, stout basally, and with sensilla-bearing small tubercles on outer aspect at base; inner edge smooth, without teeth or sharp projections. Labiomaxillary region (fig. 16) not fused, semisclerotized at base of head capsule; maxilla distinct, with elongate, spiculate, orally directed apical lobe; maxillary palpus small, about as long as basal diameter, well defined, and bearing tight cluster of numerous sensilla; palpus situated at base of apical maxillary lobe and mesad of hypostomal groove; labium in front of labial palpus somewhat protuberant, as seen in lateral view, nonspiculate; labial palpus similar to maxillary palpus,

positioned as in figures 16–18. Hypopharynx bilobed, nonspiculate, and unsclerotized; hypopharyngeal groove distinct. Salivary opening contiguous to hypopharyngeal groove (in contrast to opening of mature larva which is borne at apex of labium, [Rozen, 1969b]).

BODY: Form (fig. 14) moderately elongate, straight; body without pronounced tubercles either laterally or dorsally; abdominal segments dorsally divided in caudal and cephalic annulets; abdominal segment X rounded, without pygopod or other special ambulatory features; venters of prothorax and abdominal segment IX not protruding. Integument without setae, but with patches of fine spicules particularly ventrally. All spiracles present, large, of about equal size, and dorsally directed (as opposed to dorsolaterally directed). Anus apparently small, apically transverse slit.

MATERIAL STUDIED: 4 first instars, Cedar Point Biological Station, Keith Co., Nebraska, collected as eggs from nests of *Anthophora occidentalis* July 15, 1988, preserved as first instars July 16, 1988 (J. G. Rozen); 1 first instar, same except collected as dead larva killed by meloid, July 18, 1988.

REMARKS: P. F. Torchio (personal commun.) in reviewing this manuscript gave the following interesting account of the function of the spinulae (an autapomorphy of the Melectini) on the head of this species: "If the splitting of the egg chorion [at time of eclosion] does not occur properly as the head capsule is moved, the larva shakes its head from side to side and the spinulae act as would a can opener in cutting through the egg chorion so that the necessary splitting of the chorion can continue via pressure applied by expansion of the first 3 body terga. . ."

Melecta separata callura (Cockerell)
Figures 23–27

DIAGNOSIS: The extremely elongate head, labral tubercles, and antennae distinguish this species from all other Melectini including *Melecta pacifica fulvida*, described below, and *M. luctuosa* (Scopoli) (Giordani-Soika, 1936).

LENGTH: 3.8–4.3 mm (N = 2).

HEAD (figs. 24–27): As described for *Xeromelecta californica* except for following: Shape more strongly prognathous, more elongate. Integument of head capsule scarcely pigmented; sclerotization apparently as described for *X. californica* except internal ridges poorly defined. Each antenna enormously long, more so than in any other melectine. Labral sclerotization apparently continuous with front of head capsule; labral tubercles longer than in any other known melectine. Maxilla with apical lobe very long, nonspiculate. Labial palpus distinct but smaller than maxillary palpus.

BODY: As described for *Xeromelecta californica* except for following: Form (fig. 23) more elongate. Integument without spicules. Anus not detected.

MATERIAL STUDIED: 2 first instars, 14.5 mi N Coalinga, Fresno Co., California, March 21, 1963, [cell] opened March 27, 1963; preserved in ethyl alcohol March 29, 1963 (R. W. Thorp). In the collection of R. W. Thorp.

REMARKS: Thorp (1969) provided a detailed account of the biology of this species attacking nests of *Anthophora edwardsii* Cresson. These specimens came from his investigations.

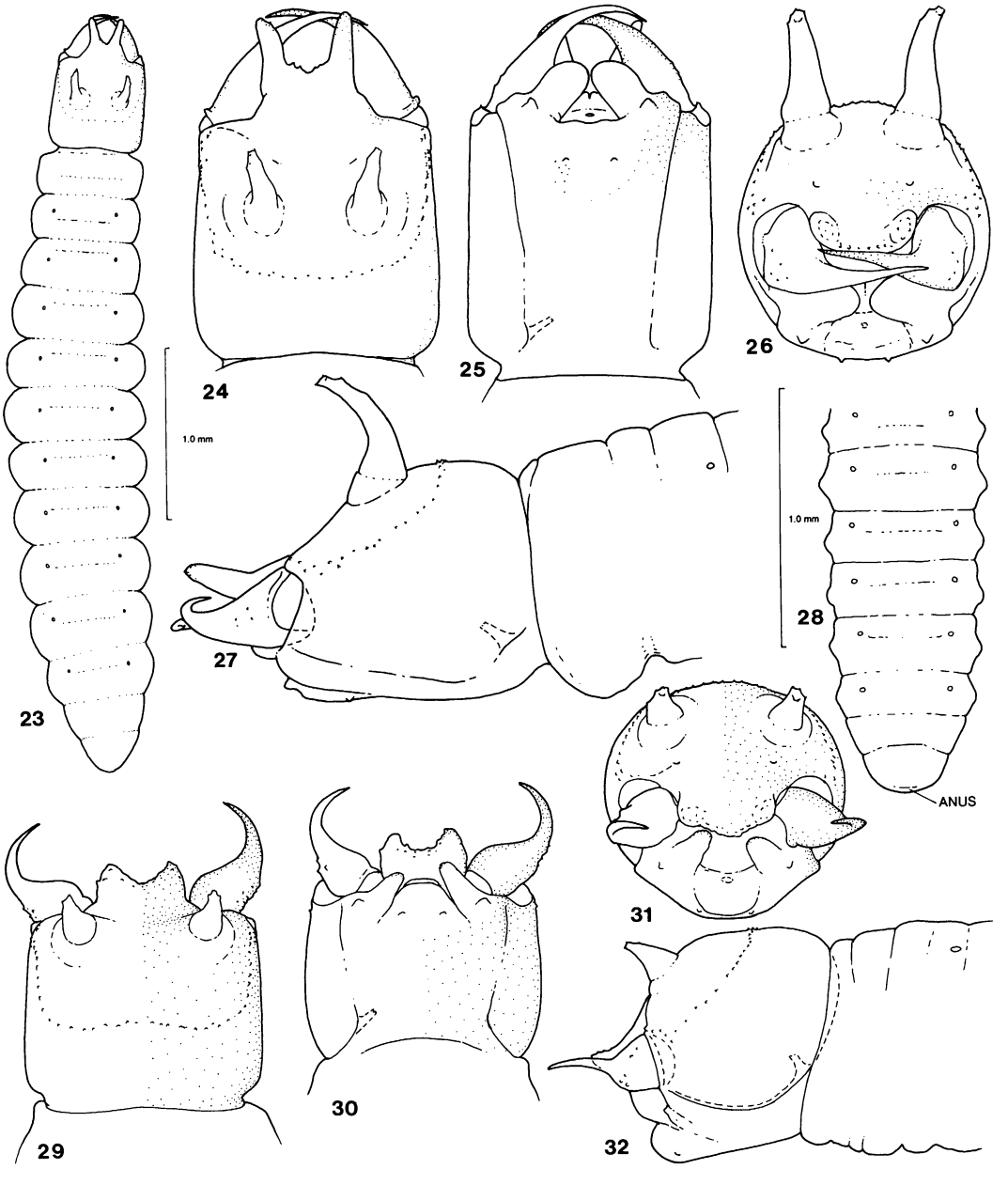
Melecta pacifica fulvida Cresson
Figures 28–32

DIAGNOSIS: This species can be easily distinguished from *Xeromelecta californica* and *Melecta separata callura* because of its shorter antennae and labral tubercles and because of its more robust head capsule as seen from above or from the sides (figs. 29, 32). Indeed the pronounced differences between the two species of *Melecta* are surprising. Its thicker antennae separate it from *Zacosmia maculata*. It appears to be most similar to *Thyreus lieftincki*, but presumably its more pronounced sensillar tubercles and anteriorly projecting labium, as seen in lateral view (fig. 32), will enable it to be recognized.

LENGTH: 2.6–3.1 mm.

HEAD (figs. 29–32): As described for *Xeromelecta californica* except for following: Head capsule not so elongate. Antenna shorter. Paired labral tubercles shorter. Maxillary lobes apparently faintly spiculate apically. Labial palpus smaller than maxillary palpus.

BODY: As seen from above (fig. 28) most



Figs. 23–27. *Melecta separata callura*, first instar. **23**. Entire body, dorsal view. **24–27**. Head, dorsal, ventral, frontal, and lateral views.

Figs. 28–32. *Melecta pacifica fulvida*, first instar. **28**. Posterior part of abdomen, dorsal view. **29–32**. Head, dorsal, ventral, frontal, and lateral views.

Scales refer to figures 23 and 28 respectively.

body segments with small paired lateral tubercle-like swellings. Anus apparently dorsal.

MATERIAL STUDIED: 2 first instars, greenhouse, USDA, Logan, Utah, June 1967 (P. F. Torchio). In the collection of P. F. Torchio.

REMARKS: Torchio and Youssef (1968) de-

scribed the egg deposition habits which resulted in the larvae described here.

Thyreus lieftincki Rozen
Figures 33–37

No first instar of this genus has been described before.

DIAGNOSIS: This larva differs from *Xeromelecta californica* and *Melecta separata callura* in that the head capsule is shorter in relation to its width, as seen in dorsal and ventral views (figs. 34, 35) and the ventral surface is less elongate as seen from the side (fig. 37). The reduced pigmentation of the head capsule and stouter antennae separate this species from *Zacosmia maculata*. It is most similar to the first instar of *Melecta pacifica fulvida* but presumably can be recognized by the features presented in the diagnosis of the latter.

LENGTH: 3.0 mm (N = 2).

HEAD (figs. 34–37): As described for *Xeromelecta californica* except for following: Head not so elongate as seen in lateral view (fig. 37). Integument scarcely pigmented except for mandibular apices; ventral integument between hypostomal grooves apparently somewhat sclerotized but pigmentation absent. Sharp-pointed spinulae of head capsule generally smaller and less pronounced; sensilla-bearing tubercles smaller, less pronounced. Tentorium weak but complete; middle part of hypostomal groove arching downward as see in lateral view rather than nearly straight; dorsal ecdysial line not visible because of lack of pigmentation elsewhere. Antenna large, but somewhat smaller than in *X. californica*. Paired labral tubercles moderately large, apically rounded. Maxillary lobes shorter, but clearly evident.

BODY (fig. 33): As described for *Xeromelecta californica*.

MATERIAL STUDIED: 2 first instars, 3 mi south Avontuur, Cape Province, Republic of South Africa, collected as eggs November 15, 1966, preserved November 18, 1966 (J. G. Rozen).

REMARKS: The mature larva of this species was described by Rozen (1969b). The biology of both this species and its host, *Anthophora braunsiana* Friese, were treated by Rozen (1969a).

Zacosmia maculata (Cresson)
Figures 38–41

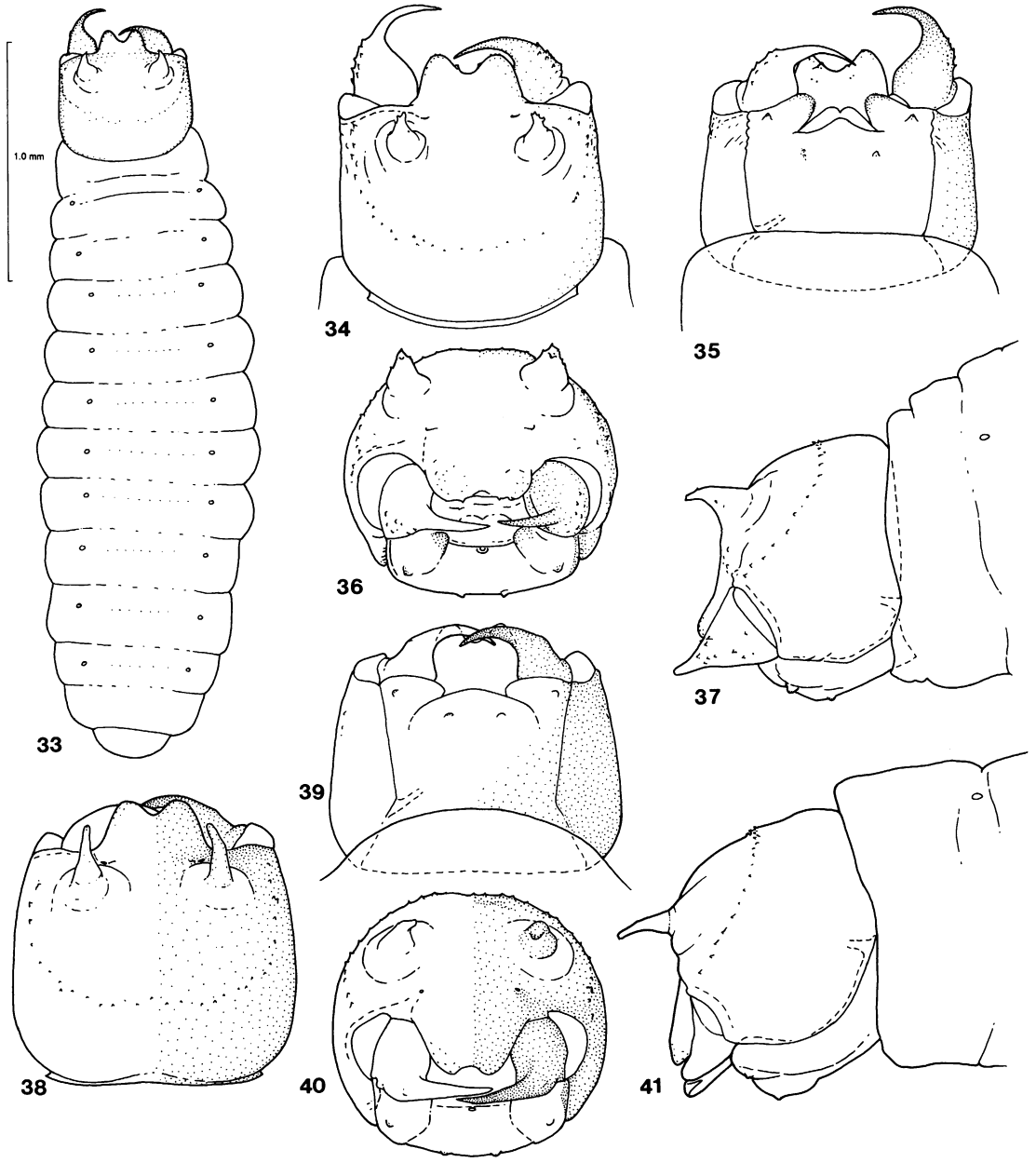
This larva was first described by Torchio and Youssef (1968).

DIAGNOSIS: This first instar is similar to those of the other melectines treated here. Its more darkly pigmented head capsule (figs. 38, 39), slender antennae, and near absence of sensilla-bearing tubercles (especially on mandibular bases) help to distinguish it. The head capsule, as seen from above or below (figs. 38, 39), is more spherical rather than quadrate and parallel-sided as in the other species. Furthermore, its antennae are directed more anteriorly, so that when seen in frontal view (fig. 40) they do not rise above the upper margin of the head.

LENGTH: 2.2 mm (N = 1).

HEAD (figs. 38–41): As described for *Xeromelecta californica* except for following: Head not so elongate as seen in lateral view (fig. 41), only vaguely quadrate, more spherical as seen from above or below (figs. 38, 39). Integumental pigmentation somewhat more pronounced than in other two species of melectines. Sharp-pointed spinulae on head capsule smaller, fewer; sensilla-bearing tubercles nearly absent. Middle part of hypostomal groove arching downward as seen in lateral view, like that of *Thyreus lieftincki*, rather than *X. californica*; dorsal ecdysial line more or less evident because of surrounding pigmentation. Antennae large but directed forward, in contrast to other two melectine taxa, so that antennae do not arise above head as seen in frontal view (fig. 40). Paired labral tubercles moderately large, apically rounded as in *T. lieftincki*. Maxillary lobes shorter, directed nearly mesially, and apparently nonspiculate; labium more forward projecting so that, as seen in ventral view (fig. 39), its apex is almost in line with apices of maxillae and hypopharynx is hidden, in contrast to less forward-projecting labia of *T. lieftincki* and *X. californica*.

BODY: Essentially identical to postcephalic regions of *Xeromelecta californica* and *Thy-*



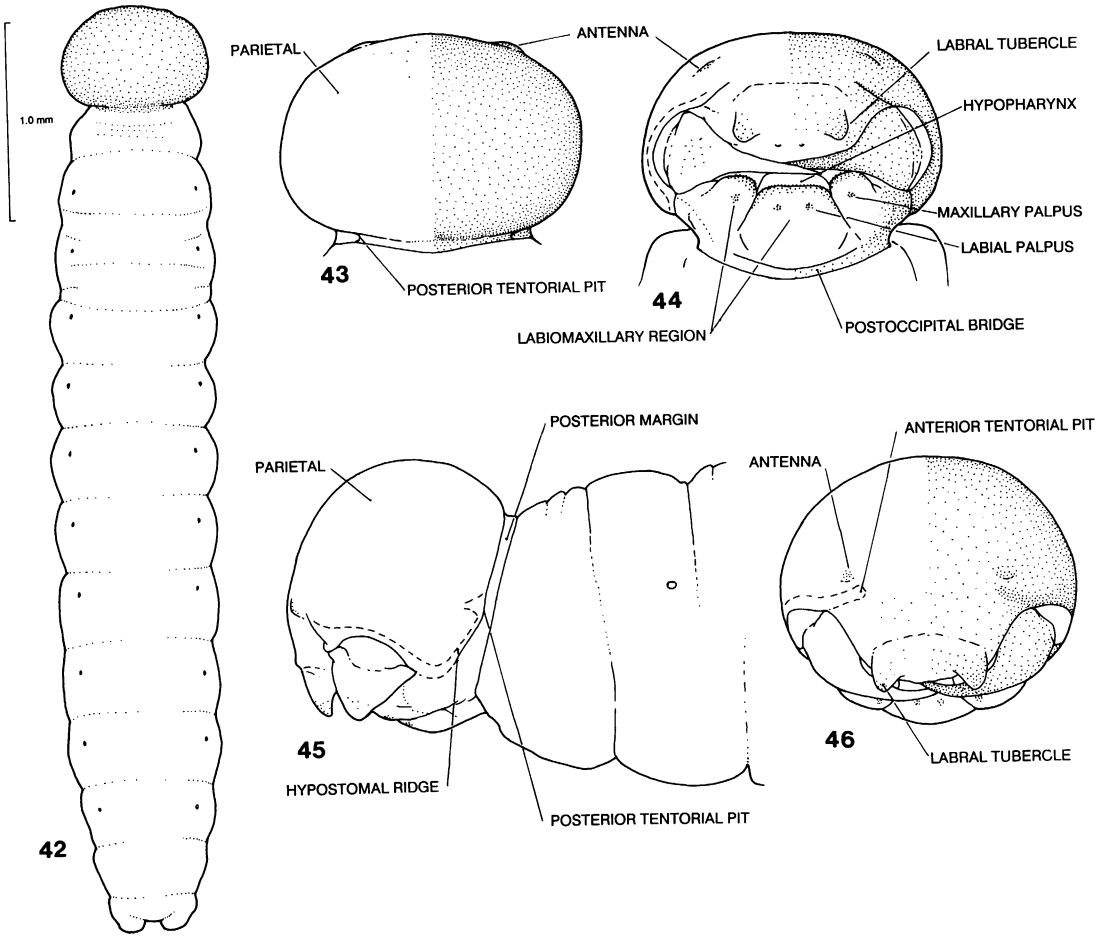
Figs. 33–37. *Thyreus lieftincki*, first instar. **33**. Entire body, first instar, dorsal view. **34-37**. Head, dorsal, ventral, frontal, and lateral views.

Figs. 38–41. *Zacosmia maculata*, head of first instar, dorsal, ventral, frontal, and lateral views. Scale refers to figure 33.

reus lieftincki; integumental spiculation reduced by comparison with *X. californica*.

MATERIAL STUDIED: 1 first instar, 1 mi north of Rodeo, Hidalgo Co., New Mexico, August 15, 1974 (J. G. Rozen).

REMARKS: Torchio and Youssef (1968) de-



Figs. 42–46. *Rhathymus bicolor*, first instar. **42**. Dorsal view of body. **43–46**. Head, dorsal, ventral, lateral, and frontal views. Scale refers to figure 42.

scribed the first instar, mature larva, and pupa of this species. Rozen (1969b) subsequently redescribed the mature larva from their material.

Description of the Rhathymini Based on First Instars

The following account is based the first instars of *Rhathymus bicolor* described below and of an unidentified species previously described by Camargo et al. (1975).

Head: Shape hypognathous; parietals swollen (fig. 43) so that capsule appears globose, unlike that of any other known cleptoparasitic anthophorid; capsule with dorsoventral distance exaggerated in relation to length because of swollen parietals. Integument of head capsule heavily sclerotized and darkly pigmented; sclerotization ending posteriorly at rear of head; sensilla not setiform, not borne on tubercles; capsule without band of spinulae across vertex. Tentorium well developed (except for dorsal arms); anterior tentorial pits distinct; posterior pits arising from hypostomal ridges and posterior thickening of head; hypostomal ridge well developed but external groove not troughlike; sclerotization of head capsule extending below ridge but most of labiomaxillary region unsclerotized; ventral sclerotized postoccipital bridge present; pleurostomal ridge well developed; epistomal ridge well developed la-

terad of anterior tentorial pits, absent mesad of pits; distinct pale median dorsal ecdysial line present; posterior margin of head capsule not forming sharp angle with hypostomal ridge, but appearing as almost straight continuation of it as seen in lateral view (fig. 45). Each antenna small, scarcely evident, fused with head capsule. Labrum bearing pair of large but not elongate, downward projecting tubercles and separated from clypeus by articulating membrane. Mandible moderately long; apex tapering to simple, sharp-pointed tip; base stout; inner edge smooth. Labiomaxillary region sclerotized only on sides of maxillae; maxilla not fused with labium except at base; maxilla with large, apically spiculated, orally directed apical lobe; maxillary palpus subapical, not projecting, represented only by cluster of sensilla; labium spiculate apically; labial palpus nonprojecting cluster of sensilla. Hypopharynx unsclerotized, bilobed, nonspiculate.

BODY: Form (fig. 42) elongate, slender, straight, without tubercles; abdominal segment X with pair of conspicuous, short, posteroventrally directed lobes, possibly but not certainly homologous with paired structures on abdominal segment X of Protepeolini and Nomadinae. Integument without setae but with patches of fine spicules. Spiracles present, of equal size, normal in position. Anus an inconspicuous, apical, transverse slit between lobe bases.

GENUS STUDIED: *Rhathymus*.

Rhathymus bicolor Lepeletier
Figures 42–46

DIAGNOSIS: This larva can be immediately distinguished from other known first instars of cleptoparasitic anthophorids because of the spherical appearance of the head capsule as seen in dorsal view (fig. 43) and its pronounced hypognathous conditions as seen in lateral view (fig. 45).

LENGTH: 4.5 mm (N = 1).

HEAD (figs. 43–46): Shape distinctly hypognathous; parietals together globose, unusually wide in relation to horizontal diameter of foramen. Integument of head capsule heavily sclerotized, moderately pigmented, except apices of mandibles darkly pigmented; ventral integument mesad of hypostomal ridges somewhat pigmented and sclerotized but fading before reaching labium except ventral extension of posterior rim of foramen apparently completely sclerotized forming postoccipital bridge (fig. 44) (hence posterior end of head a complete sclerotized ring); apices of labral tubercles vaguely pigmented; other areas of head unpigmented. Visible setae absent; head capsule without spinulae (in contrast to ring of spinulae in Melectini); sensilla minute, not borne on small tubercles. Tentorium complete except for dorsal arms, well developed; anterior tentorial pits moderate in size; posterior pits at end of hypostomal ridge; hypostomal ridge well developed, not associated with external groove, as in Epeolini and Melectini, extending downward almost ventrally from posterior pit and bending forward immediately in front of posterior mandibular articulation; integument near ridge not pebbled, wrinkled, or in other ways sculptured; sclerotization of head capsule extending mesad of (below) ridge, as described above; distance between hypostomal ridges great compared with Epeolini; pleurostomal ridge well developed; epistomal ridge well developed laterad of anterior tentorial pits, absent mesad of pits. Parietal bands absent. Antenna small, scarcely evident except for tight cluster of sensilla which are not borne on tubercles. Labrum separated from clypeus by articulating membrane; paired labral tubercles large (fig. 46), conical, downward directed, bearing many small sensilla on anterior surfaces. Mandible elongate, sharp-pointed, apically attenuate, basally stout, without tubercles on outer aspect at base; inner edge smooth, without teeth or sharp projections. Maxillae and labium not greatly fused, mostly separate as seen in ventral view (fig. 44); maxilla with large, spiculate, orally directed apical lobe; maxillary palpus faintly if at all projecting but easily recognized by close cluster of sensilla; palpus subapical in position of maxilla; labium projecting in front of labial palpi as seen in ventral view (fig. 44), so that hypopharyngeal groove and opening of salivary gland not visible from below; labial apex strongly spiculate; palpus similar to maxillary palpus. Hypopharynx very short so that opening of salivary duct and mouth close to each other; hypopharynx nonspiculate, unsclerotized,

apparently somewhat bilobed; hypopharyngeal groove distinct, but difficult to see because of being so close to mouth. Salivary opening immediately in front of hypopharyngeal groove, not visible in views illustrated.

BODY: Form (fig. 42) elongate, straight, without tubercles laterally or dorsally; abdominal segments perhaps divided dorsally into caudal and cephalic annulets, but demarcation vague; abdominal segment X bearing pair of short but large, posteroventrally directed lobes (presumably ambulatory features); venters of prothorax and abdominal segment IX not protruding. Integument without setae but with patches of fine short spicules in many areas; spicules especially well developed on posteroventral lobes of abdominal segment X and parts of abdominal segment IX. All spiracles present, about equal in size, moderately small, and dorsolaterally directed (rather than dorsally directed). Anus an inconspicuous, apical, transverse slit between bases of ambulatory lobes.

MATERIAL STUDIED: 1 first instar, Maracas Valley, Trinidad, April 7, 1965, from nest of *Epicharis rustica* (F. D. Bennett).

REMARKS: The host cell from which the specimen came bore a small hole near the center of the closure, and the vacated chorion remained attached to the inner surface of the closure. Further details on the biology of this species will be presented elsewhere.

Camargo et al. (1975) described and illustrated the first instar of *Rhathymus* sp. Their figure 13 of a recently eclosed larva shows no differences between their species and *R. bicolor*. However, their figure 10 apparently depicts a subsequent instar; compared with a first instar, its mandibles are less attenuate, its palpi project farther, and the parietal bands are evident.

DESCRIPTION OF THE ISEPEOLINI BASED ON THE FIRST INSTAR

Both Michener (1957) and Oliveira (1966) described the first instar of *Isepeolus viperinus* (Holmberg).

HEAD: Shape prognathous, elongate, and, unlike that of any other Nomadinae or other hospicidal anthophorid, strongly dorsoventrally flattened; parietals not swollen. Integument of head capsule heavily sclerotized and pigmented; unlike that in any other known cleptoparasitic anthophorid, sclerotization extending posteriorly over anterior part of prothorax; head capsule with sensilla setiform according to Michener (1957) and Oliveira (1966), but these setae apparently mostly lost on specimen examined here; only sensilla at base of mandibles borne on small tubercles; capsule without ring of sharp-pointed spinulae across vertex. Tentorium incomplete; anterior tentorial pits small but present; small posterior tentorial pits present in vague hypostomal ridges on ventral side of head well anterior to posterior margin of head sclerotization; labiomaxillary region sclerotized and fused with head capsule, unlike that in Nomadinae but similar to that in Ericrocidini; internal head ridges mostly obscure because of heavy sclerotization; pale median dorsal ecdysial line absent; angle formed by posterior margin of head and hypostomal groove in lateral view unknown because these ridges not evident. Each antenna moderately small, well defined, anteromesally directed, and fused with head capsule. Labrum sclerotized, fused with clypeus; small labrum bearing single conspicuous median tubercle and therefore unlike that of any known cleptoparasitic anthophorid. Mandible attenuated, slender apically, not stout as in Ericrocidini; inner edge smooth. Labiomaxillary region completely fused, sclerotized, and highly modified; maxillary palpus faintly produced; labial palpus not produced, represented only by sensilla. Hypopharynx apparently an unpigmented paired attenuated structure immediately below mouth.

BODY: Form elongate, straight, not tapering posteriorly, most segments laterally rounded; abdominal segments IX and X fused, somewhat similar to condition in the Ericrocidini but fusion even more complete, without pygopod or other ambulatory modifications. Integument with a few setae especially on the anterior part, unlike that in any cleptoparasitic anthophorid except *Protepeolus* (which uniquely has elongate, setiform dorsal body spicules). All spiracles present; those of abdominal segment VIII enlarged, situated at posterior margin of segment, as is characteristic of Ericrocidini. Anus not evident.

GENUS STUDIED: *Isepeolus*.

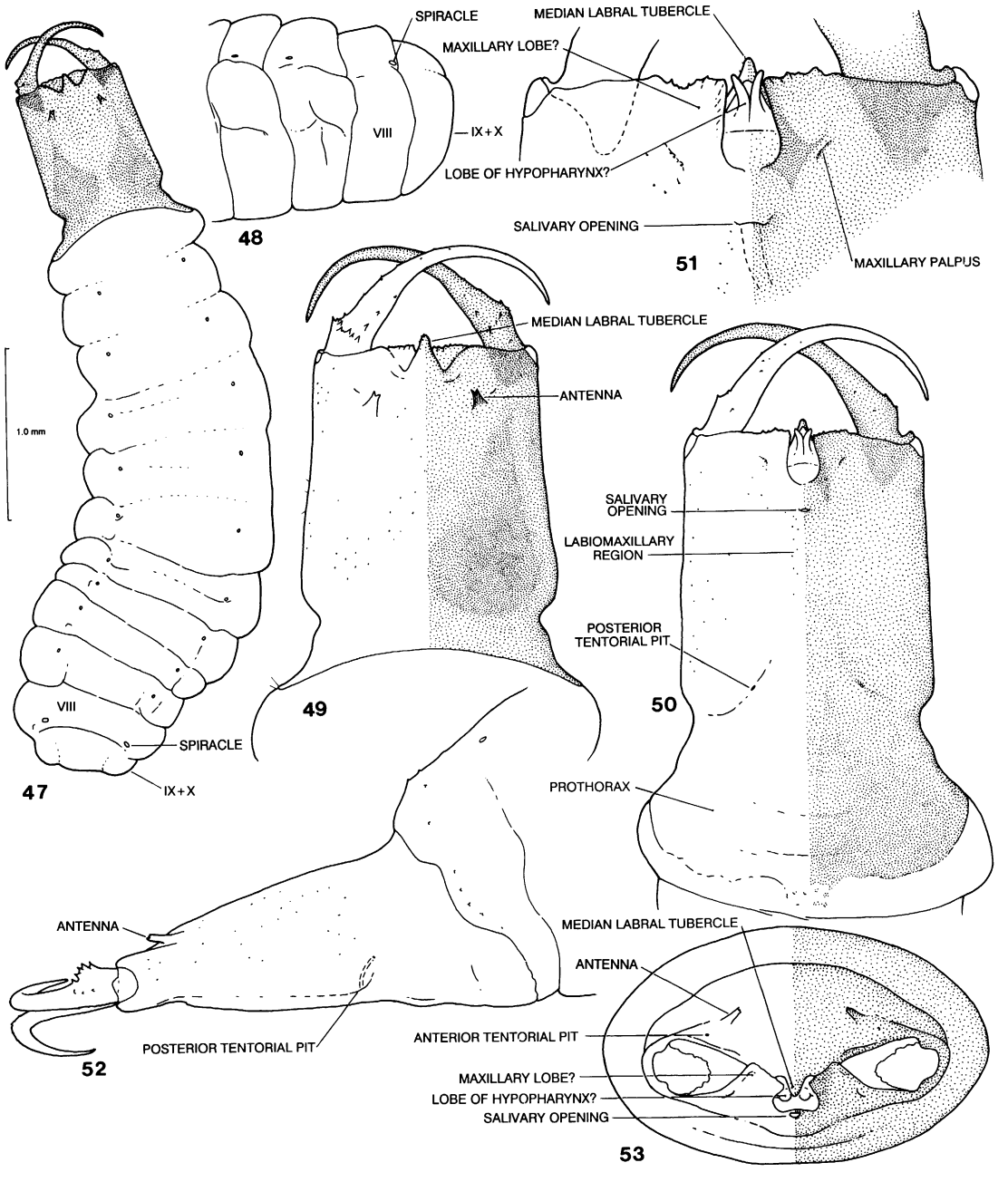
Isepeolus viperinus (Holmberg)
Figures 47–53

The redescription of this species is based on the specimen studied by Michener (1957).

LENGTH: 4.6 mm (N = 1).

HEAD (figs. 49–53): Shape strongly prognathous, very strongly dorsoventrally flattened especially anteriorly, so that head seen in lateral view (fig. 52) wedge-shaped; head capsule elongate both ventrally and dorsally; sides nearly parallel in front of posterior constriction, converging slightly anteriorly; foramen narrower than maximum width of head capsule, as seen from above or below (figs. 49, 50) but head not constricted posteriorly as seen in lateral view (fig. 52). Integument of head capsule and also ventral surface of head heavily sclerotized, darkly pigmented, i.e., labiomaxillary region sclerotized and completely fused with head capsule; sclerotization of ventral surface of head extending forward and joining with sclerotization of front of head capsule mesad of mandibular bases and laterad of presumed unpigmented hypopharyngeal region; integument of head nearly smooth; presumed hypopharynx and epipharyngeal surface of labrum unpigmented and unsclerotized (fig. 51); unlike in other known hospicidal first instar anthophorids, sclerotization of head extending posteriorly onto prothorax both dorsally and especially ventrally (figs. 49, 50). Visible setae mostly absent, although few short setiform sensilla obvious on labrum (both Michener, 1957, and Oliveira, 1966, illustrated the head capsule as bearing rather long, conspicuous setae; these no longer present on specimen studied here, presumably having been lost after preservation); head capsule without spinulae; integument of antennae, apex of labrum, and base of mandibles with numerous fine sensilla; sensilla at base of mandibles borne on small tubercles; integument of head capsule dorsally and laterally with sensilla, presumably alveolae of missing setiform sensilla. Tentorium incomplete; anterior tentorial pits small (fig. 53); anterior arms weak and short; posterior pits in faint ridge presumably representing junction of hypostomal ridge and posterior thickening of capsule; these pits far forward of posterior edge of sclerotization of head (figs. 50, 52); hypostomal ridge obscure because of thickening of head capsule except in vicinity of posterior tentorial pit; hypostomal groove absent; pleurostomal and hypostomal ridges obscure; ecdysial line not evident. Parietal bands not evident. Each antenna (figs. 49, 52) small, projecting sharply anteromesally; antennae behind anterior edge of head capsule, hence not projecting beyond dorsal mandibular articulation, as seen in lateral view (fig. 52), not arising above vertex as seen in frontal view; each antenna strongly dorsoventrally flattened, smooth except for sharp-pointed, apical bifurcation as seen from above (fig. 49). Labral sclerotization continuous with that of frons and clypeus; labral apex produced as single median tubercle bearing sensilla. Mandible slender, elongate, sharp-pointed, evenly tapering except for somewhat expanded base bearing small tubercles; inner edge smooth, without teeth or projections. Labiomaxillary region (fig. 50) fused and sclerotized; maxillary palpus (fig. 51) small, slightly produced as weak oblique ridge; apex of maxilla (fig. 51, maxillary lobe?) produced anteromedially as flat sclerotized continuation of ventral surface of head to form serrated-crenulated anterior edge of head between labrum and base of mandible (see Remarks below); hence anterior edges of maxillae apparently serving as knifelike, destructive edge of head against which closing sickle-shaped mandibles force host immature (analogous to knifelike edge of hypopharynx of Epeolini (Rozen, 1989b); anteromedially apices of maxillae curving downward along mesal edges that surround unsclerotized structures (fig. 51, hypopharynx?) in vicinity of mouth; labial palpus not produced, represented only by one or more sensilla behind salivary opening as confirmed by small but distinctly produced palpus of second instar in similar position. Hypopharynx presumably unsclerotized, unpigmented, attenuate paired processes extending forward nearly as far as labral apex; hypopharyngeal groove not clearly evident. Salivary opening (fig. 51) very large, directed somewhat anteriorly, and connecting to very wide salivary duct.

BODY: Form (fig. 47) elongate, parallel-sided, somewhat truncate posteriorly because of modifications of terminal abdominal segments and lateral body swellings; body with-



Figs. 47–53. *Isepeolus viperinus*, first instar. **47**. Entire body, dorsal view. **48**. Apex of abdomen, lateral view. **49, 50**. Head, dorsal and ventral views. **51**. Anterior part of head, enlarged, ventral view. **52, 53**. Head, lateral and frontal views. Scale refers to figure 47.

out dorsal tubercles but most segments swollen laterally; abdominal segments perhaps divided into weak cephalic and caudal annulets dorsally; abdominal segments IX and X (figs. 47, 48) greatly fused; presumably IX represented laterally by swollen lobes between which is small segment X; distinct intersegmental line between IX and X not ev-

ident; pygopod not present; venters of prothorax and abdominal segment IX not protruding. Integument with a few, very fine, short setae and mostly without spicules except for scattered indistinct patches. All spiracles present; those of thorax and abdominal segments I–VII subequal in size, dorsally directed, and in normal position; spiracles of abdominal segment VIII unusually large, situated near posterior edge of segment, and posteriorly directed; spiracular tracheae of segments VIII much larger than those of other segments and connecting to very large tracheal trunks, hence larvae appearing to be semi-metapneustic. Anus not evident.

MATERIAL STUDIED: 1 first instar, Araucaria, Paraná, Brazil, January 13, 1956 (C. D. Michener) from cell of *Colletes kerri* Moure. In the collection of the University of Kansas, Lawrence, currently on deposit at the American Museum of Natural History.

REMARKS: A second instar as well as several subsequent instars were preserved in the same vial as this specimen. In sharp contrast to the first instar, head capsules of the other specimens were pale and weakly sclerotized, and the mandibles were not strongly curved. These facts indicate that only the first instar is hospicidal.

The anatomy of the first instar is highly modified and the homologies of some of the mouthparts may be open to reinterpretation. The maxillary palpi are clearly identifiable, and therefore the sharp-edged, anteromesal extensions of the anterior ventral head surface in front of them appear to be the maxillary apices (lobes). Because the pharynx lies immediately above the elongate, paired unpigmented median processes, they are considered to be the hypopharynx.

DESCRIPTION OF THE ERICROCIDINI BASED ON FIRST INSTARS

First instars of the Ericrocidini have not been previously described except for a brief account of *Mesoplia* sp. (Vinson et al., 1987).

HEAD: Shape strongly prognathous, elongate, not strongly dorsoventrally flattened although slightly so in *Aglaomelissa*; parietals not swollen. Integument of head capsule heavily pigmented and sclerotized; sclerotization ending posteriorly at rear of head, not extending over anterior part of thorax (as in *Isepeolus*); sensilla nonsetiform, not borne on tubercles except in *Ericrocis*; capsule without band of spinulae across vertex (as found in Melectini) but head tubercles of *Ericrocis* superficially like spinulae. Tentorium, except for dorsal arms, complete (not known for *Ericrocis*); anterior pits distinct but small; posterior pits in hypostomal groove anterior to posterior margin of head; troughlike hypostomal groove present and granulate in *Ericrocis*, absent in *Aglaomelissa* and *Mesoplia*; hypostomal ridge only vaguely visible as somewhat darker area; entire ventral surface of head (labiomaxillary region) sclerotized and darkly pigmented; pleurostomal and epistomal ridges scarcely evident because of head sclerotization; distinct pale dorsal ecdysial line present; posterior margin of head capsule at right angle to hypostomal ridge as seen in lateral view (fig. 59). Each antenna completely fused to head capsule, large, anterodorsally directed, slightly to considerably dorsoventrally flattened. Labrum sclerotized, fused with clypeus, vaguely bilobed apically. Mandible robust, elongate, evenly tapering entire length from stout base; inner edge without teeth or sharp projections (ventral mandibular surface of *Aglaomelissa* uniquely with elongate sulcus). Labiomaxillary region greatly fused and sclerotized so that even palpi scarcely if at all recognizable. Hypopharynx bilobed, nonsclerotized, unpigmented.

BODY: Form moderately elongate, straight, without dorsal or lateral tubercles except: (1) lateral swellings on abdominal segments IX and X of at least *Aglaomelissa* and *Mesoplia* giving larva truncated appearance, and (2) *Ericrocis* with pair of knoblike lateral prothoracic tubercles; lateral swellings on abdominal segment X possibly assisting in crawling. Integument without setae, with some fine spiculation. All spiracles present; those of thorax of *Aglaomelissa* and *Mesoplia* somewhat reduced in size; those of abdominal segment VIII of *Aglaomelissa* and *Mesoplia* situated near posterior edge of segment, directed somewhat posteriorly, and larger than others; all spiracles of *Ericrocis* presumably subequal in size and normal in position. Anus faintly visible at least on one species, situated apically between lateral lobes of segment X.

GENERA STUDIED: *Aglaomelissa*, *Mesoplia*, and *Ericrocis*.

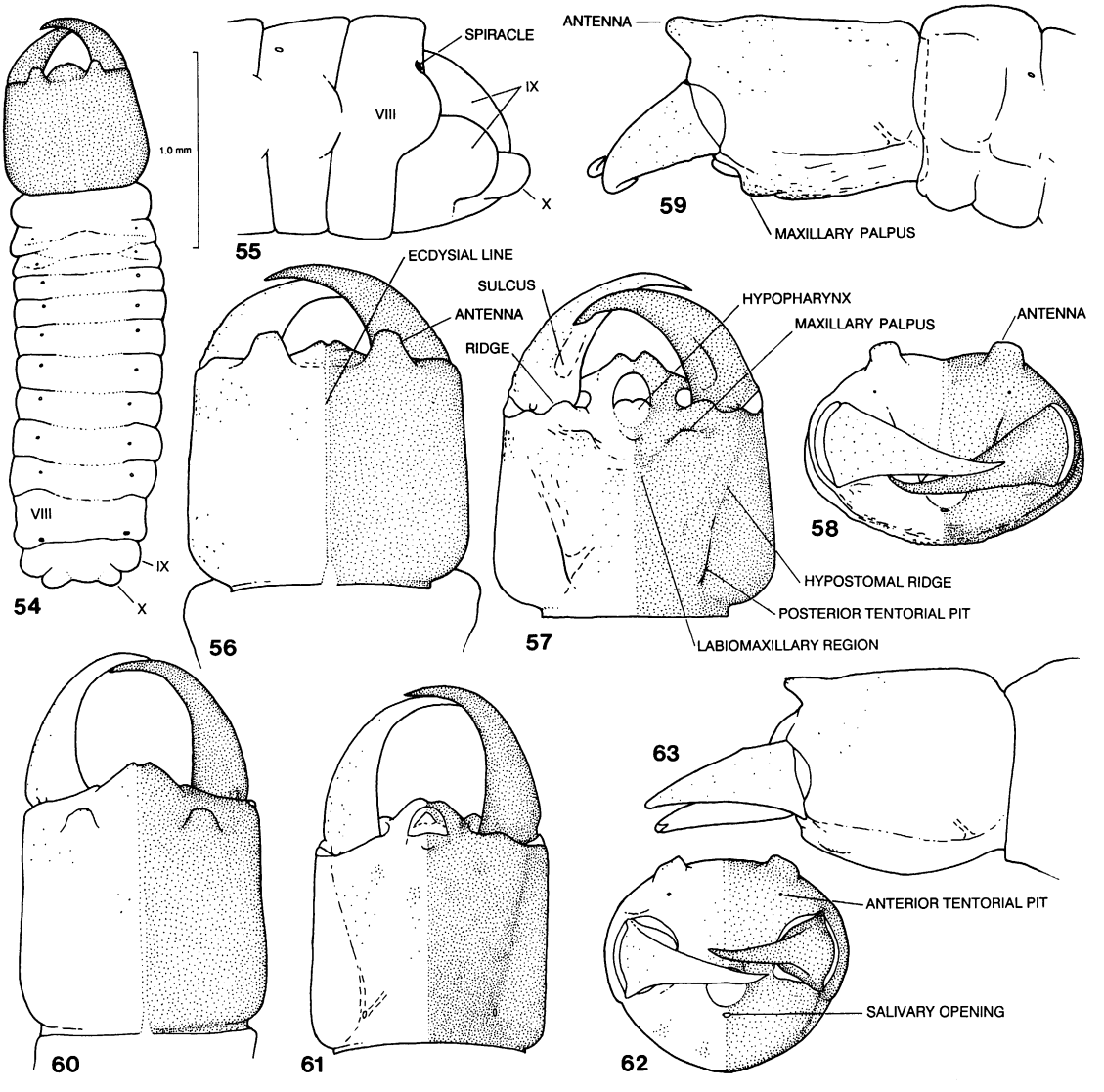
Aglaomelissa duckei (Friese)
Figures 54–59

Several females of *Mesoplia rufipes* and one of *Aglaomelissa duckei* were collected at the nesting site of *Centris carrikeri* where this larva was recovered. This first instar was identified by the fact that it differs from the first instars (described below) clearly associated with adults of *M. rufipes* from another locality on Trinidad.

DIAGNOSIS: First instars of *Mesoplia rufipes* and *Aglaomelissa duckei* are similar in most respects. They can be distinguished from one another because the mandible of *A. duckei* alone bears an elongate sulcus on its ventral surface (fig. 57), its head is more dorsoventrally flattened (fig. 58, in contrast to fig. 62), its mandible is more robust and less curved apically (figs. 56, 57, in contrast to figs. 60, 61), and its antennal apex extends well beyond the dorsal mandibular articulation (fig. 59, in contrast to fig. 63). The first instar of *Ericrocis* (figs. 64–67) can immediately be separated from first-stage larvae of *Aglaomelissa* and *Mesoplia* because of its conspicuous, sharp-pointed head tubercles, the paired knoblike prothoracic tubercles, nonfusion of the dorsal and ventral head sclerites mesad of the mandibular bases, and salivary opening not surrounded by the labiomaxillary sclerotization.

LENGTH: 3.4 mm (N = 1).

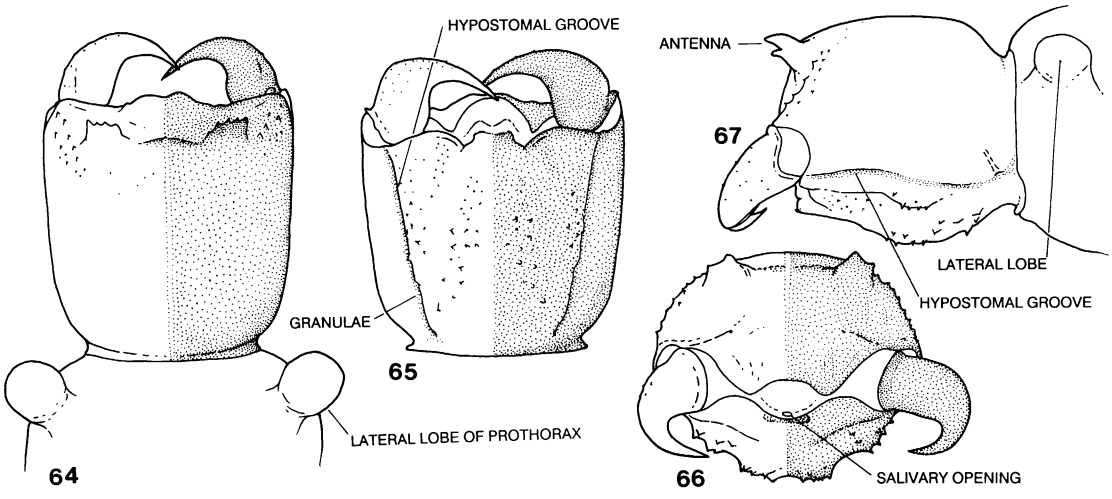
HEAD (figs. 56–58): Strongly prognathous, dorsoventrally flattened (area between antennae and posterior margin of head nearly flat as seen in lateral view, fig. 59, elongate ventrally as well as dorsally, with sides nearly straight but converging slightly anteriorly; foramen narrower than width of head capsule. Integument of head capsule heavily sclerotized, darkly pigmented; mandibles darkly pigmented throughout; ventral surface of head between hypostomal ridges sclerotized and darkly pigmented; this sclerotization extending forward and joining sclerotization of front of head capsule mesad of mandibular bases and laterad of hypopharynx; integument of head capsule behind mandibular corium finely pitted; that of ventral surface of head (labiomaxillary region) unevenly wrinkled; only hypopharynx and epipharyngeal surface of labrum unpigmented and unsclerotized, as seen in ventral view (fig. 57). Visible setae absent; head capsule without spinulae (as found in Melectini); integument of antennae, anterior edge of labrum, outer surfaces of mandibles, and labiomaxillary region with numerous fine sensilla which are generally not borne on small tubercles (those at base of mandible borne on minute tubercles). Tentorium, except for dorsal arms, complete, but weak; anterior tentorial pits moderate in size; posterior pits in hypostomal grooves well in front of posterior edge of head as seen in ventral view (fig. 57); hypostomal ridge obscure because of thickness of head integument; external hypostomal groove absent; distance between ridges large compared with that of Epeolini; integument mesad of hypostomal ridge and immediately behind base of mandible produced into transverse ridge, suggestive of (but presumably only analogous to) hypostomal process of Epeolini (Rozen, 1989b); this ridge perhaps part of maxilla as suggested by counterpart in *Isepeolus viperinus* (which see); pleurostomal ridge scarcely evident because of thickness of head sclerotization; epistomal ridge absent; pale dorsal ecdysial line conspicuous from rear of head capsule to apex of labrum because of surrounding pigmentation. Parietal bands not evident. Each antenna large, projecting anterodorsally beyond dorsal mandibular articulation as seen in lateral view (fig. 59), rising above vertex as seen in frontal view (fig. 58); antenna smooth (not knurled as in Melectini), slightly ventrodorsally flattened, apically rounded and not conical; antennal sensilla not borne on small tubercles. Labral sclerotization continuous with that of clypeus and frons, not separated by articulating membrane or ridge. Labrum without distinct tubercles but with apical pair of obtuse projections bearing numerous sensilla, possibly homologous with labral tubercles. Mandible robust, elongate, sharp-pointed (although extreme apex of left mandible slightly expanded, fig. 57); mandible evenly tapering its entire length, not stout at base and slender apically; inner edge smooth, without teeth or sharp projections (except for extreme apex of left mandible, as described above); ventral



Figs. 54–59. *Aglaomelissa duckei*, first instar. **54**. Entire body, dorsal view. **55**. Apex of abdomen, lateral view. **56–59**. Head, dorsal, ventral, frontal, and lateral views.

Figs. 60–63. *Mesoplia rufipes*, head of first instar, dorsal, ventral, frontal, and lateral views. Scale refers to figure 54.

surface of each mandible, unlike that of other cleptoparasitic anthophorid tribes, with elongate sulcus (fig. 57) which may accommodate apex of opposing mandible when it is closed (this suggests that lower mandible [the left one on this specimen] closes more tightly than the upper, for there is no dorsal sulcus on either mandible which would seemingly be necessary if both mandibles closed tightly at the same time). Labiomaxillary region greatly fused and extensively sclerotized, so that even palpi are nearly indistinguishable; maxillary palpus vague, anteriorly declivous area laterad of salivary opening, recognized by numerous sensilla; labial palpus indistinguishable except apparently for grouping of sensilla behind and mesad of maxillary sensilla; palpi fused (not articulating) with labiomaxillary



Figs. 64–67. *Ericrocis lata* or *pintada*, head of first instar, dorsal, ventral, frontal, and lateral views.

region. Hypopharynx unsclerotized, unpigmented, and bilobed; hypopharyngeal groove not evident. Salivary opening in sclerotized area, somewhat posterior to hypopharynx.

BODY: Form (fig. 54) elongate, parallel-sided, posteriorly somewhat truncate because of modifications of last two abdominal segments; body without tubercles laterally or dorsally except abdominal segment IX protuberant on sides and abdominal segment X with posterolateral swelling on each side; abdominal segments not dorsally divided into caudal and cephalic annulets; abdominal segment X dorsally fusing with segment IX so that intersegmental line indistinguishable; pygopod, as in Epeolini, not present, but paired lateral swellings may serve ambulatory function; venters of prothorax and abdominal segment IX not protruding. Integument without setae, mostly nonspiculate although a few indefinite patches seen dorsally toward abdominal apex. All spiracles present and most directed dorsally; those of thorax somewhat smaller than those of abdomen; those of abdominal segment VIII unusual in that they are situated toward posterior edge of segment, are larger than others, and are directed somewhat posteriorly; spiracular tracheae of segment VIII of greater diameter than those of other segments. Anus apparently an indistinct scar apically situated between protruding lateral lobes of abdominal segment X.

MATERIAL STUDIED: 1 first instar, Maracas Valley, Trinidad, West Indies, collected as egg on February 23, 1966; preserved as larva on February 24, 1966 (F. D. Bennett, J. G. Rozen), from cell of *Centris carrikeri*. Associated adult identified by Roy R. Snelling.

REMARKS: As will be reported elsewhere, the egg from which this larva emerged was attached by one end to the closure, an indication that the egg was deposited through an opening in the closure after the cell had been sealed.

Mesoplia rufipes (Perty)
Figures 60–63

DIAGNOSIS: See Diagnosis of *Aglaomelissa duckei*.

LENGTH: 4.8 mm (N = 1).

HEAD (figs. 60–63): As described for *Aglaomelissa duckei* except for following: Sides of head capsule subparallel. Integument of head capsule behind mandibular corium smooth; ventral surface of head between hypostomal ridges (labiomaxillary region) smooth; sensilla of mandibles not borne on small tubercles. Each antenna large, but smaller than that of *A. duckei*, not projecting beyond dorsal mandibular articulation as seen in lateral view

(fig. 63). Mandible directed anteriorly (fig. 63) (rather than anteroventrally, fig. 59), less robust than that of *A. duckei*, slightly more elongate, and more strongly curved apically than basally but evenly tapering; ventral surface of each mandible smooth, without elongate sulcus. Maxillary and labial palpi recognized only by grouping of sensilla (fig. 61).

BODY: As described for *Aglaomelissa duckei* except for following (specimens distorted, hence not illustrated): Form perhaps tapering slightly posteriorly, more so than in *A. duckei*. Integument bearing finely spiculated ventral patch on most body segments. Thoracic spiracles somewhat smaller than abdominal ones; abdominal ones small except spiracles on abdominal segment VIII much larger, about twice diameter of others; these spiracles on posterior edge of segment, directed posteriorly, as in *A. duckei*, and with enlarged tracheae. Anus not certainly visible on distorted specimen.

MATERIAL STUDIED: 1 first instar, 1 cast first instar exuviae still attached to chorion, Hollis Reservoir, Trinidad, West Indies, March 7, 1968, preserved March 10, 1968 (J. G. and B. L. Rozen) from nest of *Epicharis albofasciata* Smith. Associated adults identified by Roy R. Snelling.

REMARKS: Three host cells were parasitized by the *Mesoplia* at this site. In two cells, a small hole was found in the center of the closure, indicating that the *Mesoplia* female made a small hole through which she introduced her egg into the cell. Further details will be published elsewhere.

Similar observations regarding egg deposition and chorion attachment to first instar were reported by Vinson et al. (1987) for an unidentified *Mesoplia*.

Ericrocis lata (Cresson) or *pintada* Snelling and Zavortink

Figures 64–67

Knowledge of the larva of this species comes from a cast first-instar integument accompanied by the second instar. Because both species of *Ericrocis* were collected at the time that the parasitized host nest was discovered, the identification of the species of cleptoparasite is uncertain.

DIAGNOSIS: See diagnosis of *Aglaomelissa duckei*.

LENGTH: Probably approximately 4.0 mm (N = 1).

HEAD (figs. 64–67): As described for *Aglaomelissa duckei* except for following: Top of head capsule as seen in lateral profile (fig. 67) curved; sides of head capsule diverging anteriorly as seen from above or below (figs. 64, 65). Although head capsule sclerotized and darkly pigmented ventrally and dorsally, pigmented sclerotization of two surfaces not fusing anteriorly mesad of mandibular bases (figs. 65, 66), unlike in other two ericrocidine species (figs. 57, 61); integument of head capsule behind mandibular corium smooth except for sharp-pointed sensilla-bearing tubercles; that of labiomaxillary region also with sharp-pointed sensilla-bearing tubercles (in addition to other sensilla). Head capsule without spinulae (but see discussion under Remarks). Condition of tentorium uncertain because only weak posterior and anterior arms extant in cast skin; external hypostomal groove conspicuous, with granulations; integument immediately behind mandible and mesad of groove not ridgelike, merely marking anterior margin of maxillary sclerotization; pleurostomal ridge and lateral arms of epistomal ridge weak but evident in relation to heavily sclerotized head. Antenna not projecting anterior to dorsal mandibular articulation as seen in lateral view (fig. 67); antenna appearing somewhat similar to that of Melectini because sensilla borne on small tubercles, but antenna strongly dorsoventrally flattened; frons between antennae produced as transverse granulated ridge. Mandibular ventral surface without sulcus. Maxillary and labial palpi not visible except perhaps for sensilla; labium immediately below (behind) salivary opening projecting as small transverse ridge bearing conspicuous granulations, unlike in any other known parasitic first instar. Salivary opening immediately above anterior labial ridge and separated from labiomaxillary sclerotization by short distance (fig. 66).

BODY: Form probably elongate and parallel-sided, as judged from cast exuviae; prothorax, unlike in any other known cleptoparasites, with pair of lateral, knoblike tubercles (figs. 64, 67) which persist in second instar; other aspects of body form uncertain

because of telescoping and wrinkling of integument, but for reasons explained in Remarks, form of posterior part of body probably similar to shapes of *Aglaomelissa duckei* and *Mesoplia rufipes*. Integument spiculate on venter of most segments. All spiracles present and subequal in size, apparently including those of abdominal segment VIII; position of spiracles of abdominal segment VIII unknown but for reasons expressed in Remarks, possibly normal, i.e., not on posterior margin of segment.

MATERIAL STUDIED: 1 cast integument of first instar, 1 mi east Douglas, Cochise Co., Arizona, August 20, 1990 (J. G. Rozen, J. Krieger), collected with 5 *Ericrocis* eggs, 1 vacated *Ericrocis* chorion, 1 *Centris* egg, and 1 live second instar of *Ericrocis* from single cell of *Centris* possibly *atripes* Mocsary.

REMARKS: The host bee, with pale mesosoma and black metasoma, was observed making the nest on August 16 but was not collected. *Centris atripes* was the commonest species present with this color pattern. The shallow nest excavated on August 20 consisted of a single cell that was heavily parasitized. The *Centris* egg as well as 5 *Ericrocis* eggs floating on or near the surface of the semiliquid provisions presumably had been killed by the first instar that had emerged from the vacated *Ericrocis* chorion and that then molted to the second instar.

The head capsule of the cast first instar exuviae was as easy to study as that of a complete first instar, and the anterior part of the body, split along the dorsal midline as far the second abdominal segment, clearly revealed the paired prothoracic lateral, knoblike tubercles. The rest of the body form was difficult to interpret because of telescoping of the cast integument. The second instar possessed posterolateral swellings on abdominal segments IX and X just as did a second instar of *Mesoplia rufipes*, suggesting that the first instar of *Ericrocis* resembles that of *Mesoplia* and *Aglaomelissa*.

The position of the last pair of spiracles on the *Ericrocis* exuviae could not be ascertained. These spiracles on the live second instar were normal in position, approximately halfway between the anterior and posterior margin of segment VIII. However, the terminal spiracles of the second instar of *Mesoplia* were clearly near to the posterior margin of segment VIII. Hence all spiracles on the first instar of *Ericrocis* may be placed normally.

The first instar of *Ericrocis* superficially resembles that of the Melectini. In addition to general head shape, the sharp-pointed tubercles on the *Ericrocis* head capsule appear to be melectine spinulae. However, they do not extend across the vertex as do spinulae in all melectines and microscopically each bears a single sensillum and not an apical rosette of points as is the case with spinulae (fig. 22). Furthermore similar sharp-pointed tubercles are also present in the labiomaxillary region of *Ericrocis*, but spinulae never appear in this region in melectines. Other features of *Ericrocis* are markedly different from the Melectini: antennae dorsoventrally flattened and fused with the integument of the head; labiomaxillary region extensively fused and sclerotized; palpi not evident.

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